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THE SYSTEMATICS AGENDA 2000 SYMPOSIUM: INTRODUCTION[1]

P. Mick Richardson[2]

The fortieth anniversary of the first Systematics Symposium was appropriately celebrated with a meeting on the subject of Systematics Agenda 2000, a published report (Anon, 1994) on a global initiative to discover, describe, and classify the world's species. Jay Savage carefully selected an array of speakers that would give the audience an overview of the diversity of systematic studies and the impact of these on the study of evolution, conservation, food supplies, disease sources, and disease prevention.

The symposium began with a presentation by Brent Mishler, "Speciation, Adaptation, and Evolution," that explained why sound phylogenetic frameworks are needed to formulate general evolutionary theories concerning basic processes such as adaptation, speciation, and extinction. This contribution is not published here (although see Mishler (1995) for further references), but the remaining six papers were submitted as manuscripts for publication. Russ Monson delivered a paper entitled "Systematics and Plant Function in a Changing Environment," which illustrated the use of phylogenetic reconstruction to test comparative hypotheses in plant physiology and developmental biology. Amy Rossman's presentation, "Wood-rotters, Leafhoppers and Systematics," coauthored by Douglass Miller, explored the role of some of the less conspicuous but specious organisms, such as insects, fungi, nematodes, and bacteria, and their beneficial, neutral, and detrimental interactions with agricultural and forestry systems. Mike Vecchione's report, "Fisheries, Systematics and Marine Diversity," coauthored with Bruce Collette, explained how systematists must disseminate their knowledge if it is to have practical effects in, for example, fisheries management. James Oliver's talk, "Ticks, Microbes and Disease," sent shivers down my spine as I recalled my unpleasant experience with Lyme disease some years ago. He informed the audience of the increasing costs of tick-borne diseases and the necessity of correct identification of the tick species and the disease organisms if a rational plan of treatment and control is to be developed. A shortage of younger taxonomists in this field is a potential problem. The daytime session was brought

[1] This and the six articles that follow it are the proceedings of the 41st Annual Systematics Symposium of the Missouri Botanical Garden, *Systematics Agenda 2000: Systematics and Society.* The symposium was held 30 September–1 October 1994 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

The symposium was supported in part by the National Science Foundation under grant number BSR89–18138. I thank Jay M. Savage, of the University of Miami, for selecting a fine diversity of speakers, Carol Davit for indispensable logistical help in organizing the symposium, John Myers for his fine illustration for the symposium brochure, and the world's numerous systematists for being such an interesting and diverse group.

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to a close by Dick Vane-Wright with a paper entitled "Death and the Compass: Systematics for Saving Life." Again, we saw how natural taxonomic hierarchies were the best methodology to use, in this case for determining priorities for the conservation of living things. Finally, the after-dinner talk, entitled "Ethnobotany for the Nineties" (but see how the published paper was transformed for the new millenium), was presented by Mike Balick; it included a fine set of examples of current ethnobotanical projects that illustrate the public's growing awareness of this branch of biological science. This was a fitting end to a stimulating meeting. I hope that you will enjoy reading the published proceedings that follow.

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THE USE OF PHYLOGENETIC PERSPECTIVE IN COMPARATIVE PLANT PHYSIOLOGY AND DEVELOPMENTAL BIOLOGY[1]

Russell K. Monson[2]

ABSTRACT

The use of phylogenetic reconstruction for the testing of comparative hypotheses is a recent development in the fields of plant physiology and developmental biology. In this review, several uses of phylogenetic information are discussed, including (1) the use of phylogenetic trees for choosing experimental systems, (2) justifying the statistical independence of compared taxonomic groups, (3) identifying evolutionary direction using outgroup analysis, and (4) studying the evolutionary tempo of physiological and developmental change. Difficulties are also discussed, especially with respect to (1) mapping continuous, physiological traits onto the discrete, binary structure of phylogenetic trees, (2) constructing trees from traits that are independent of the physiological and developmental characters being mapped, and (3) respecting the statistical nature of phylogenetic trees. The bulk of the review is devoted to several examples from the literature that illustrate the power of a phylogenetic perspective in comparative studies. Reviewed examples include (1) elucidation of a novel pyrophosphate-dependent phosphofructokinase in the glycolytic pathway of phosphate-stressed plants in the Brassicaceae, (2) evolutionary pattern in the origins of polyploid endosperm in angiosperms, (3) adaptive radiation of Hawaiian Island plants into dry habitats, and (4) evolutionary pattern in the origins of C_4 photosynthesis. The fields of systematics, comparative physiology, and developmental biology will continue to merge as their common reliance on phylogenetic perspective increases.

The purpose of this review is to describe aspects of the past, present, and future relationship between two historically disparate disciplines—comparative plant systematics and comparative plant physiology and development. Researchers in plant systematics focus on the pattern of evolutionary diversification. Researchers in plant physiology and plant developmental biology focus on the products of evolutionary diversification—functional mechanisms, structural attributes, and their relationships to genetic and environmental controls. The nexus among these disciplines occurs through a need to understand the role of evolutionary constraint in dictating patterns of adaptation, the timing and rate of phenotypic evolution, and the evolutionary interactions among phenotypic traits.

Historically, one can recognize several connections between the fields of comparative systematics and comparative functional biology. As examples, consider the numerous studies that originated in Sweden with Turreson (1922) and in the United States with Clausen et al. (1940, 1948). The focus of these studies was firmly embedded in the evolutionary process: to uncover the cohesive and divergent forces that maintain the structure of taxonomic units while at the same time allowing for diversification and speciation. A principal component of these early studies included comparisons among plants from different geographic locations that were grown in common environments. The goal pursued in these "common-garden" studies was to partition the influence of genetic and environmental influences on character expression. During the birth of modern comparative physiology, and to a lesser extent developmental biology, scientists discovered that the same common-garden approach could be used to standardize the influence of environment, while observing inherited differences in the adaptive responses of plants (e.g., Mooney & Billings, 1961; Björkman & Holmgren, 1963). Fur-

[1] The author is grateful for the thoughtful comments, discussions, and unpublished material provided by Ray Huey, Michael Grant, Manuel Lerdau, William Bowman, Ned Friedman, Richard Olmstead, Robert Robichaux, Bill Plaxton, Suzanne Warwick, Todd Dawson, and Paul Teese. Special thanks are due to Michael Grant, Brian Farrell, and Richard Olmstead for their helpful collaboration in providing the *Flaveria* phylogeny. Thanks are also due to the sponsors and leaders of the Systematics Agenda 2000 effort and the Organizing Committee of the Missouri Botanical Garden's 41st Annual Systematics Symposium. The author's research discussed in this paper was supported by NSF grants BSR-8604960 and BSR-8911433.

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thermore, by choosing congeneric and confamilial groups for their comparisons, these mechanistic biologists were using phylogenetic perspective as they observed the products of common descent, identified examples of convergent evolution, and isolated patterns of adaptation. Thus, at its inception, modern comparative plant physiology had definitive links with comparative plant systematics. Unlike researchers in comparative systematics, however, the focus of comparative physiologists was not the evolutionary process in relation to natural taxonomic units, but rather the nature of mechanistic adaptations and their relationship to environmental extremes.

Since these pioneering studies, researchers in physiology and developmental biology have strayed from their phylogenetic, comparative origins, embracing instead the implicit assumption that functional responses to the environment are the products of natural selection. When it comes to interpreting evolutionary patterns in functional traits, formal hypothesis testing has often given way to intuition and adherence to an adaptational doctrine. This tendency has been criticized in past essays (e.g., Gould & Lewontin, 1979). The potential contributions of phylogenetic reconstruction and the comparative method to formal hypothesis testing in physiological and developmental biology have only recently been revisited (e.g., Felsenstein, 1985; Huey, 1987; Harvey & Pagel, 1991; Garland & Carter, 1994; Lauder et al., 1995). There is little doubt that as more biologists become aware of the useful deductions that can be made using phylogenetic data, a remarriage will be witnessed between the fields of comparative systematics and comparative physiology and development.

On the Different Natures of Comparative Systematics and Comparative Physiology/Development

In comparative systematics, trait variation is used to study natural relationships among different groups of organisms. In comparative physiology and development, natural relationships among organisms are used to study the nature and functional significance of traits. Thus, although researchers in both fields draw upon the same puzzle pieces (variation in organismic traits), those in one discipline use the pieces to assemble the puzzle, while those in the other discipline use the completed puzzle to study the pieces.

In focusing on adaptation, comparative physiologists ask the question: does physiological variation among organisms show a pattern that is consistent with the process of natural selection (Feder, 1987)? Pattern is typically measured as the functional attributes of organisms native to different environments. If the pattern correlates with enhancement of growth and persistence across an environmental gradient, then the pattern is ascribed to natural selection and is taken as adaptive. Recent studies, however, have revealed phylogenetic history to be as likely a constraint on pattern variation as is natural selection (Huey, 1987; Garland & Carter, 1994; Lauder et al., 1995). Disentanglement of phylogeny and selection is only accomplished through reliance on comparative systematics and the existence of accurate phylogenetic reconstruction. The integration of comparative systematics with comparative physiology and development is an exercise in mapping functional traits onto established phylogenetic trees. Several methods have been developed to accommodate such mapping and the accompanying statistical analysis (Felsenstein, 1985; Harvey & Pagel, 1991; Brooks & McLennan, 1991).

There are some potential pitfalls that must be recognized before one can successfully engage in the activity of phylogenetic mapping. For example, many comparative physiologists and developmental biologists may not recognize the tentative nature of phylogenetic trees. At first appearance, such trees reflect firm, definitive relationships, especially from the perspective of mechanistic biologists who are accustomed to observing the discrete conclusions of manipulative experiments. It is important, however, to recognize the statistical nature of phylogenetic trees. A phylogenetic tree is essentially the solution of greatest parsimony, given knowledge about a particular set of measured, shared traits among an assumed set of related taxa. In many cases a tree constructed from assumptions of maximum parsimony will poorly reproduce the alleged phylogeny (Fiala & Sokol, 1985; Rohlf et al., 1990; Lamboy, 1994). Phylogenetic trees have conclusive confidence limits that should be honored when framing conclusions about evolutionary patterns.

As a second example of issues dealing with phylogenetic mapping, comparative physiologists and developmental biologists must recognize disparities in the nature of traits that are frequently studied. Comparative systematics is based on the use of discrete, binary traits, the raw material of cladistic construction. Comparative mapping of physiological and developmental traits also requires that they have clearly delineated limits. There are examples of such traits (e.g., the presence or absence of the C_4 photosynthetic pathway), though most physiological traits, and to a lesser extent developmental

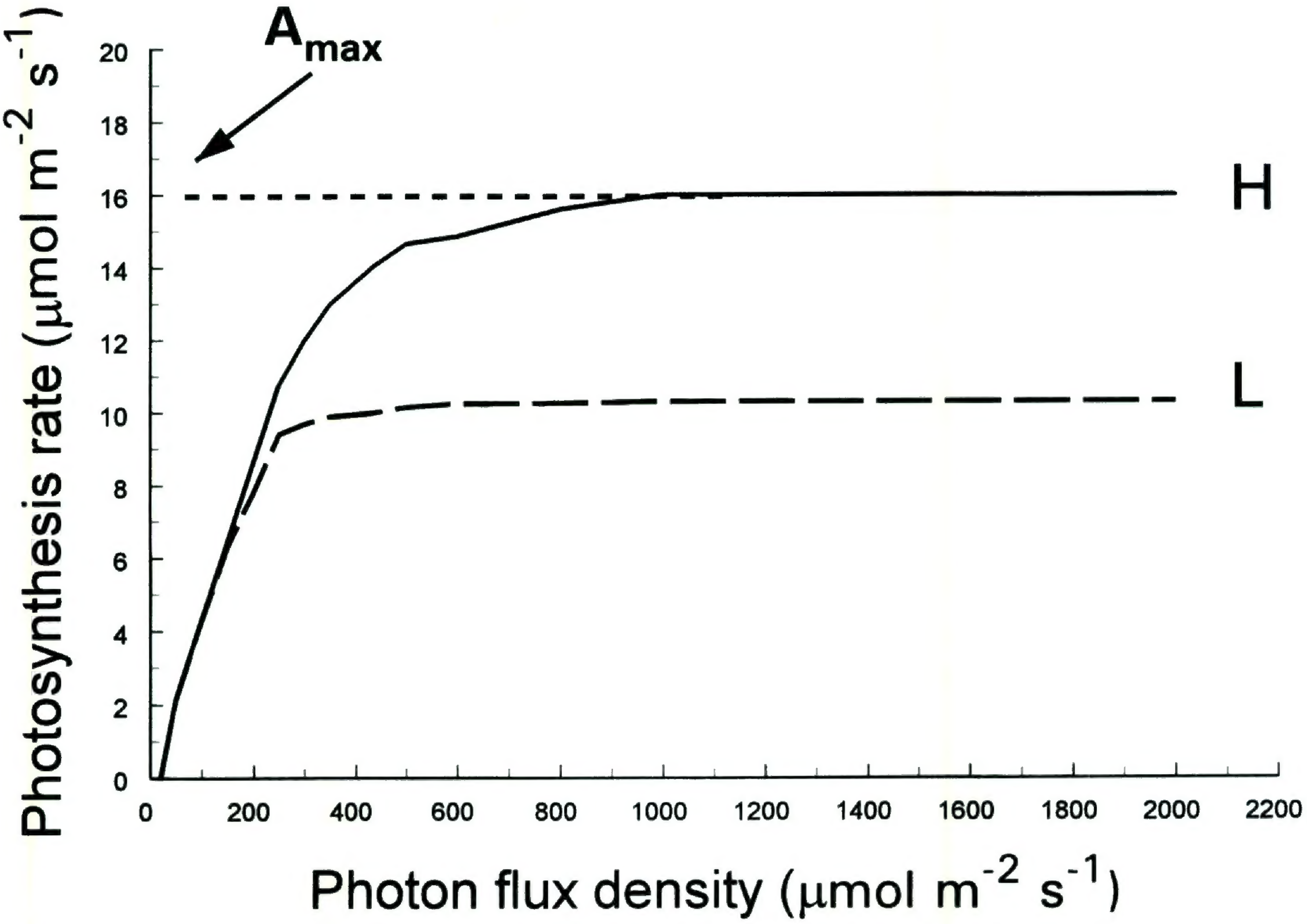

Figure 1. Hypothetical responses of photosynthesis rate to incident photon flux density in a high-light grown leaf (H) and a low-light grown leaf (L). The results demonstrate variability in photosynthesis rate as a function of the immediate (or instantaneous) light environment and the past (or growth) light environment. One commonly used index of photosynthesis rate in studies of genotypic differences is the maximum photosynthesis rate (A_{max}).

traits, are continuous and show plasticity in their responses to the environment. This leads to difficulties in the process of mapping. As an example consider the case for photosynthesis rate, one of the most commonly studied characters in comparative physiology. Within a plant, maximum photosynthesis rates can vary considerably (by up to a factor of 10) among leaves that develop in different parts of a plant's canopy (e.g., Fig. 1). By studying the cause of such variation comparative physiologists can gain insight into interactions between the photosynthetic process and a plant's environment, in this case the light environment. Yet this same variation creates difficulties in assigning discrete character values for phylogenetic mapping.

In some way, the influence of environment on character expression must be standardized. Phylogenetic reconstruction is only meaningful if the mapped traits reflect genotypic comparisons without environmental influence on character variability. One way this is commonly accomplished in studies of comparative physiology is to compare maximum observed values for some process (e.g., A_{max} in Fig. 1). It is reasoned that if the expression of a trait is measured at its maximum for all compared taxa, then variability in the measurements reflect genotypic differences. In practice, difficulties arise in determining the species- and trait-specific conditions that foster maximum expression of a trait. For some traits (e.g., resource acquisition rates) maximum expression may come with environmental conditions that maximize growth, whereas with other traits (e.g., mechanisms of stress tolerance) it may come under environmental conditions that minimize growth.

One final issue to deal with in terms of phylogenetic mapping is the need to construct phylogenetic trees from traits that are not mechanistically linked to those being mapped. This concern is minimized when trees are constructed from molecular markers (though one can imagine gene sequences in which molecular variability is reflected in enzymatic variability). Trees based on morphological traits carry greater risk in this respect. Lack of independence between traits used in tree construction and those mapped onto the tree would decrease the likelihood of reproducing the true phylogeny for the mapped trait.

On Specific Issues That Can Be Addressed Using a Phylogenetic Perspective

PHYLOGENY AND THE CHOICE OF EXPERIMENTAL TAXA

Phylogenies can be used to provide direction in the choice of experimental systems—allowing for the choice of taxa that are closely related or more distantly related. This allows investigators to maximize the possibility that the traits being compared are the products of common descent in the case of closely related groups, or convergent evolution in the case of distantly related groups. Through the a priori choice of groups with contrasting phylogenetic patterns, investigators can study the relative roles of phylogenetic inertia versus selection in influencing the evolution of functional traits.

Traditional choices of experimental systems in comparative functional biology have been driven by considerations of environment (Huey, 1987; Lauder et al., 1995). With respect to plants, the paradigm of choice has stated that adaptive responses to environment are best observed in extreme habitats. Thus, adaptive responses to high temperature are best studied in hot, desert habitats, whereas adaptive responses to cold temperatures are best studied in cold, tundra environments. This approach contains a compelling dose of intuition and logic. However, it also perpetuates some dangerous and shortsighted assumptions. One principal assumption is that any intuitively beneficial aspect of a functional attribute is the product of selection in response to the most common, and potentially stressful, environmental extreme. A corollary to this assumption is that, with respect to influences on phenotype, selection in a plant's current environment has overshadowed historical events in the acquisition of traits from past ancestors. These assumptions feed the adaptationist program discussed above. This current environment-oriented approach has little provision for phylogenetic constraint or inertia. This is where a phylogenetic perspective can contribute to adaptive analysis. By choosing groups based on criteria of both environment and the availability of phylogenetic reconstructions, one can conduct truly synthetic analyses of (1) the relative roles of selection versus phylogenetic constraint, and (2) the relationship of traits to the current versus past environment.

PHYLOGENY AS A GUIDE TO STATISTICAL ANALYSIS

Phylogenetic relationships can be used to justify statistical patterns among experimental groups being compared. It is an unattainable goal for comparative biologists to obtain groups that are completely independent in terms of past history. There is always going to be some degree of common, hierarchical descent in a system characterized by a monophyletic cladogram. Phylogenetic connections interfere with statistical assumptions of independence (Clutton-Brock & Harvey, 1984; Felsenstein, 1985; Martins & Garland, 1991). Basically, this is a "degrees of freedom" issue that becomes especially relevant in attempts to construct correlations among co-occurring traits or relate the expression of a trait with environmental variability. By ignoring phylogenetic relatedness, investigators tend to inflate the potential for Type I errors (wrongful rejection of the null hypothesis), reduce the power of their statistical conclusions, and increase inaccuracies in estimating correlation coefficients (Martins & Garland, 1991). The only groups that appear to be immune from such phylogenetic influences are those characterized by early diversification followed by long periods of phylogenetic stasis (so-called "star" phylogenies in Felsenstein, 1985) (see Martins & Garland, 1991).

Several methods have been proposed to deal with the problems of phylogenetic interdependence. The simplest method, though not the most accurate, is to center the analysis on higher taxonomic units, which will presumably possess weaker phylogenetic interdependence in terms of the traits they exhibit (Crook, 1965; Clutton-Brock & Harvey, 1984). This method does not completely deal with the issue of phylogenetic connections, however, since even the higher levels will be interdependent to some degree. An approach that deals more directly with phylogenetic connections was first proposed by Felsenstein (1985) and modified in various ways by others (e.g., Huey & Bennet, 1987; Grafen, 1989). In essence, this approach takes advantage of expected variance of character change to compute standardized, independent contrast values from the measured comparative data. Such contrast values can then be subjected to standard statistical tests of significance. Even with this approach, however, uncertainties exist due to limited knowledge about phylogenetic branch lengths and their relationship to the rate and pattern of evolution—specifically, whether trait diversification has occurred in a gradual or punctuated pattern (Martins & Garland, 1991).

PHYLOGENY AND THE DETERMINATION OF EVOLUTIONARY PATTERN

Phylogenetic trees represent maps from which one can polarize patterns of adaptive diversification. Polarization involves determination of the se-

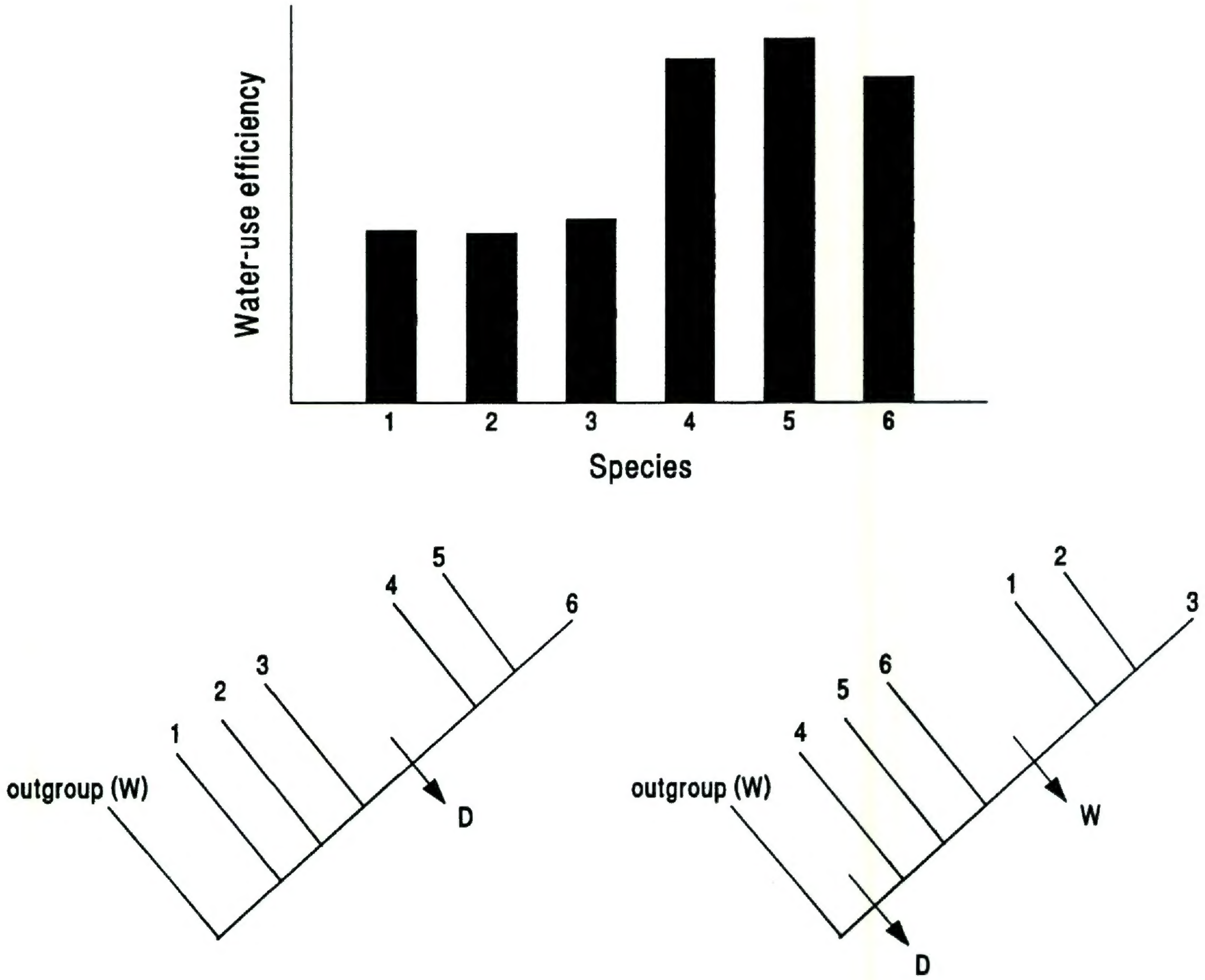

Figure 2. Hypothetical water-use efficiencies measured for six different plant species (upper panel). The lower two trees demonstrate how evolutionary patterns in this physiological character can be polarized with respect to ancestral and derived traits using outgroup comparison. In both cases the outgroup is assumed to occur in wet habitats (W). Those species exhibiting lower water-use efficiencies are assumed to also occur in wet habitats, whereas those that exhibit higher water-use efficiencies occur in dry habitats (D). In the tree on the left, a single transition is found to occur as species radiated into dry habitats and evolved higher water-use efficiencies. In the tree on the right, a transition has occurred early during diversification of the group, followed by a later reversal.

quential origins of traits relative to patterns of taxonomic diversification. The origins of traits are polarized through comparison with ancestral outgroups. Without outgroup polarization, it is impossible to determine whether a trait represents the ancestral or derived state. This use of phylogeny is illustrated in Figure 2 for a hypothetical study of photosynthetic water-use efficiency. Without phylogenetic analysis, it is not possible to determine whether high or low water-use efficiency represents the ancestral state in this group of species. Two alternative phylogenies are presented, each of which leads to a different conclusion concerning the evolutionary pattern in this trait.

In addition to polarizing single traits, outgroup analysis and phylogenetic mapping also provide a means for studying the evolutionary interactions between, or among, multiple traits. By simultaneously mapping two or more traits, one can gain insight into how the evolutionary appearance of one trait may have influenced the appearance of a different trait. Alternatively, the appearance of traits can be mapped simultaneously with major ecological shifts (e.g., shifts in habitat type, phenology, or community structure). With respect to plants, this approach may be particularly useful in deducing the relationships between functional and life-history traits, as well as between functional and structural traits.

The use of phylogenetic trees for the study of evolutionary patterns represents the most fundamental of all symbiotic connections between the disciplines of comparative systematics and comparative functional biology. This is the connection

that is destined to draw the most attention from comparative physiologists and developmental biologists. As is evident in the following sections, this approach has great power to provide new insight into the processes and patterns of functional adaptation.

PHYLOGENETIC RECONSTRUCTION AND THE DETERMINATION OF EVOLUTIONARY TEMPO

With appropriate calibration, phylogenies can be used to assess rates of evolution. Rates of evolution can provide insight into patterns of adaptive radiation and their underlying processes such as natural selection and genetic drift. Temporal calibration of phylogenies can be accomplished through paleontological dating, the use of molecular clocks (e.g., dePeer et al., 1993), or the application of statistically based trajectory models to the variance among measured characters (e.g., Lande, 1985; Lynch, 1990; Martins, 1994). The use of dated phylogenies to derive temporal patterns of evolution in functional traits has not been great. There are several complexities that still need resolution before such use is likely to increase. For example, molecular clocks are typically based on neutral traits. However, it is likely that most functional traits have, at some time in their past, been the subject of selection—a process that may have accelerated evolutionary change relative to neutral markers. Additionally, there are uncertainties in the clocks themselves and their application to phylogenetic reconstruction. These uncertainties include heterogeneity in the rate of nucleotide base substitution depending on the DNA environment (Saccone et al., 1989), errors due to interactions between the choice of nucleotide sequence and the method of tree reconstruction (Zharkikh & Li, 1993), and the influence of certain functional traits (e.g., generation time and metabolic rate) on nucleotide substitution rates (Martin & Palumbi, 1993). If such complexities can be resolved, evolutionary clocks could become valuable tools as comparative biologists address the issue of future environmental change and its influence on evolutionary patterns in the Earth's biota.

On the Use Of Systematic Information Systems for the Discovery and Inventory of Unique Biochemical and Physiological Processes

Phylogenetic trees provide maps of historical linkages among groups of organisms. As with any map, phylogenetic trees can provide direction and orientation for searches of unique functional processes. It is not uncommon to find investigators screening an entire genus to determine the extent of distribution in some functional trait or identify possible comparative systems in which the trait differs. Such an approach has been taken, for example, in the identification of *Chlorella* species possessing the ability to utilize bicarbonate as an inorganic carbon source (Miyachi et al., 1985) and the assessment of phytochelatin (heavy-metal binding peptides) distribution within various groups of plants (Gekeler et al., 1989). Recognition of phylogenetic pattern in the distribution of phytochemicals has existed for many years. In fact, phytochemical distribution represents the foundation for chemosystematics, a central discipline within the broader field of comparative systematics. In many instances the chemicals of systematic interest also have roles in plant adaptation. Terpenes and alkaloids, for example, exhibit strong phylogenetic affinities and serve an adaptive role in deterring herbivory (Banthorpe & Charlwood, 1980; Lerdau et al., 1994). Quaternary ammonium and tertiary sulfonium compounds are distributed along conservative phylogenetic lines and have important roles in plant responses to salinity and water stress (Rhodes & Hanson, 1993). Numerous other examples of phytochemicals that have dual importance to comparative systematics and comparative physiology can be described (e.g., flavonoids, cyanogenic glycosides). In all these examples the systematic approach has played an obvious role in expanding the list of species that possess the chemical of interest and in establishing correlations between taxonomic and ecologic distributions.

One recent case in which phylogenetic knowledge has had an obvious influence on trait discovery concerns the inducible pyrophosphate-dependent phosphofructokinase that was recently reported in *Brassica nigra* (L.) W. D. J. Koch (Theodorou & Plaxton, 1993, 1994). Theodorou and Plaxton (1994) suggested that this enzyme confers an adaptive advantage under phosphate stress by allowing glycolytic processing of fructose 6-phosphate in the face of reduced ATP availability. Following a protocol typical of comparative physiologists, Plaxton's group recently screened other plant species to assess overall distribution of the inducible enzyme (W. Plaxton, Queen's University, pers. comm.). Their search revealed its presence at relatively high constitutive levels in tobacco and tomato cells, but the absence of phosphate-stress inducibility. A similar pattern of constitutive presence, without inducibility, was found in other *Brassica* species thought to be closely allied with *B. nigra* (e.g., *B. oleracea* L. and *B. rapa* L.). Thus,

it appeared that the induction mechanism was isolated to *B. nigra*, being absent even from congeners. At this point Plaxton's group initiated discussions with Suzanne Warwick, a systematist who had recently constructed a phylogenetic tree of *Brassica* and related taxa through the use of cpDNA markers (Warwick & Black, 1993). From the molecular phylogeny it was clear that *B. nigra* is more closely allied with three members of the genus *Synapis*, than *Brassica* (Fig. 3). Plaxton's group has recently surveyed the two species of *Synapis*, *S. alba* L. and *S. arvensis* L., which appear to share close affinities with the re-aligned *B. nigra*. Both *Synapis* species exhibit the inducible pyrophosphate-dependent phosphofructokinase.

This example provides three important conclusions concerning the use of phylogenetic trees in studies of comparative physiology and developmental biology. First, it is clear that phylogenetic trees can be useful in directing the search for novel biochemical, physiological, and developmental processes. Second, this example illustrates the potential two-way exchange of information in collaborations between systematists and functional biologists. In this case the distribution of the pyrophosphate-dependent phosphofructokinase provides independent support for the taxonomic realignment of *B. nigra* as suggested by the molecular phylogeny. Finally, it should be clear that the effective use of systematic information systems by comparative physiologists and developmental biologists requires that taxonomy reflect phylogeny. The fact that *B. nigra* was traditionally classified with *Brassica*, rather than with *Synapis*, caused this biochemical search to stray from the correct phylogenetic path.

One area in which a phylogenetic approach is currently missing, but potentially beneficial, is the study of herbicide resistance in weedy, agricultural pests. In the past 25 years it has become obvious that the continued use of herbicides on agricultural fields has resulted in the evolution of several herbicide-resistant weed species (Warwick, 1991; Holt et al., 1993). Apparently, there is considerable interspecific and interpopulation variability in the likelihood of evolving herbicide resistance. It is unknown to what extent such variability is due to differences in selection regime, population genetic structure, or phylogenetic constraint. A systematic approach would be of obvious benefit in partitioning the influences of selection versus phylogeny, though to date no such approaches have been attempted. An example of the potential use of comparative systematics to the question of herbicide resistance can be seen in the case of triazine resistance in *Amaranthus*. Within North America numerous cases of triazine resistance have been reported in *A. powellii* S. Watson and *A. hybridus* L., the two less widespread species of North American weedy amaranths (Hill, 1982). Triazine resistance has only been reported in one population of the more widespread species, *A. retroflexus* L. Although the data are incomplete, there is reason to hypothesize that the two minor species will usurp the ecological dominance of the widespread species in the face of continued heavy herbicide use (see Gressell & Segal, 1982). This issue is complicated by the fact that European populations of *A. retroflexus* appear more likely to develop triazine resistance compared to North American populations, a situation common to weedy species that find themselves outside their native ranges (Gressell & Segal, 1982). This problem begs for the inclusion of a phylogenetic perspective. The question of whether one species is more or less constrained by its phylogeny to evolve herbicide resistance would appear to be fundamental to understanding and predicting future patterns in biological responses to herbicide applications.

On the Use of Phylogenetic Analysis to Discern Evolutionary Patterns in Plant Development and Function

Phylogenetic trees provide comparative biologists with an important tool to uncover and polarize evolutionary pattern in functional traits. Through an examination of pattern comes insight into the evolutionary constraints that have influenced, and will continue to influence, functional responses to the environment. In the following paragraphs examples are provided to illustrate the use of phylogenetic trees to study evolutionary patterns in plant physiology and development.

Ephedra and Double Fertilization

For many years it was thought that a defining trait of angiosperms was the process of double fertilization during reproduction. Friedman (1990) has recently challenged this dogma through definitive observations of double fertilization in *Ephedra*, a non-flowering seed plant. Phylogenetic trees constructed from numerous traits, including molecular markers, have placed *Ephedra* as a basal member of the Gnetales, the group of extant non-flowering seed plants most closely allied to the angiosperms (Doyle & Donohue, 1986). Using these phylogenetic relationships as a guide, Friedman (1992) was able to demonstrate that the likely homolog to angiosperm endosperm is the supernumerary-embryo product of the second fertilization in *Ephedra* (Fig.

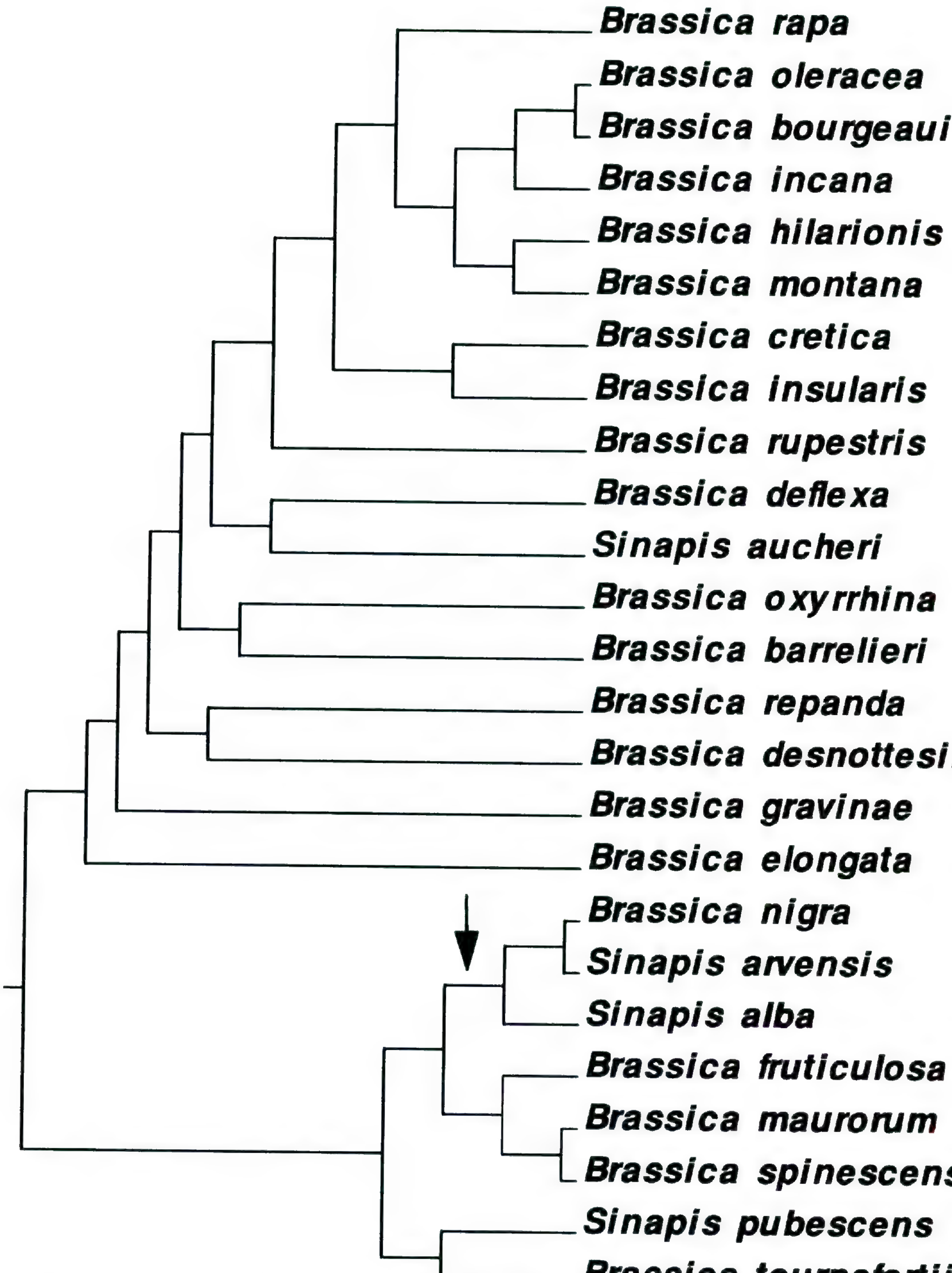

Figure 3. Phylogenetic relationships among members of subtribe Brassicinae (Cruciferae, tribe Brassiceae) based on cpDNA restriction mapping. The tree has been "pruned" from the more complete analysis presented in Warwick and Black (1993), such that only species in *Brassica* and *Sinapis* are shown. The arrow marks the currently known distribution of the inducible PPi-dependent phosphofructokinase as determined by W. Plaxton (Queens University, Ontario, pers. comm.).

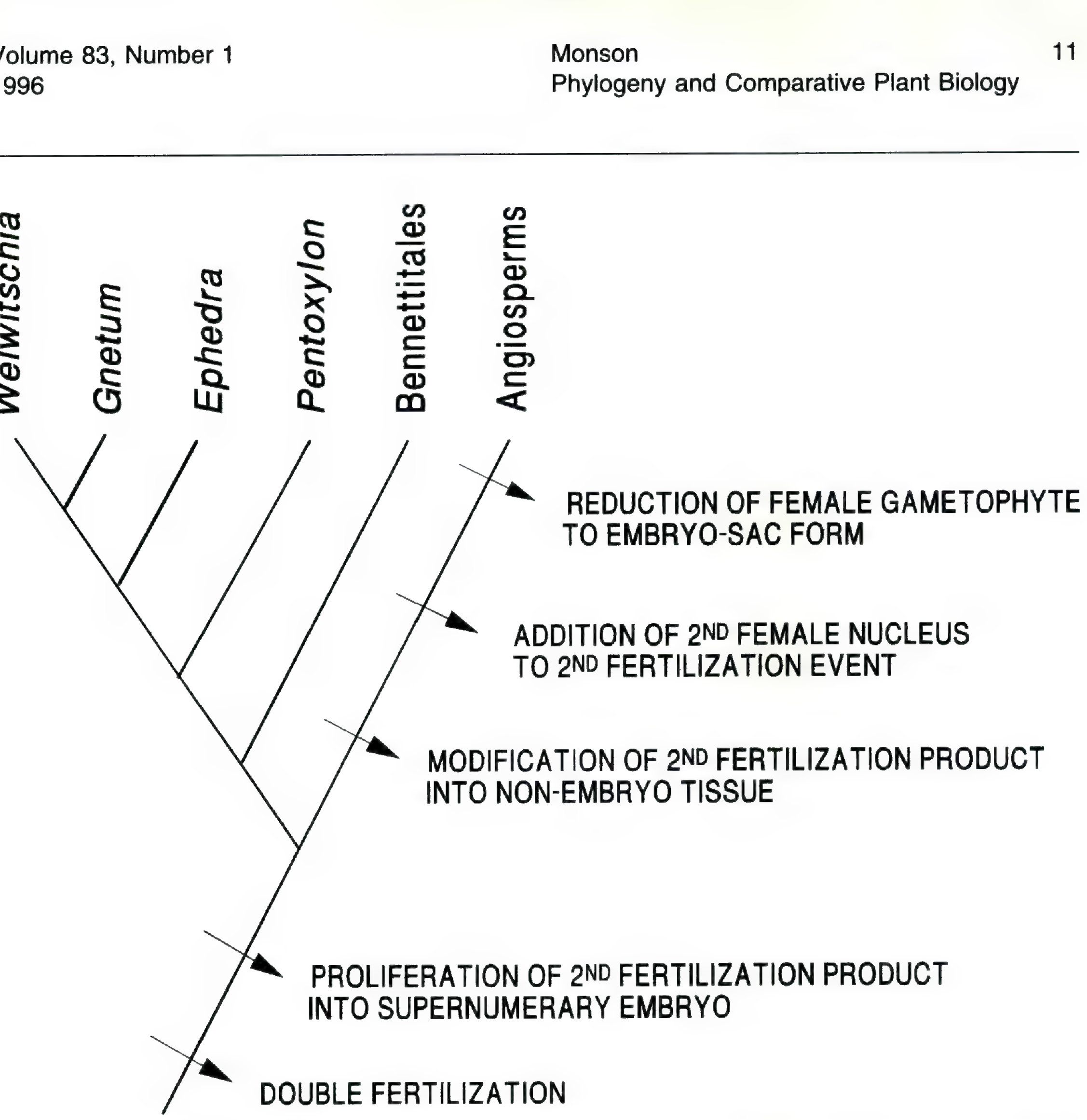

Figure 4. Phylogenetic mapping of double fertilization and the evolution of polyploid endosperm in the Anthophytes, including the Gnetales (*Ephedra, Gnetum, Welwitschia*), the fossil groups *Pentoxylon* and Bennettitales, and the angiosperms. Following observations by Friedman (1990, 1992) it is concluded that double fertilization occurs prior to divergence of the angiosperms, but the evolution of polyploid endosperm occurred after divergence. Redrawn from Friedman (1992).

4). The supernumerary embryo functions to nourish the primary embryo—an act of apparent "altruism" that raises questions about the role of kin selection in the evolution of developmental pathways (Friedman, 1992).

ADAPTIVE RADIATION IN THE HAWAIIAN ISLANDS

Recent collaborative studies between Robert Robichaux (a comparative physiologist and ecologist) and Bruce Baldwin (a comparative molecular systematist) provide an example of how phylogenetic trees can direct the study of physiological adaptation. The Hawaiian silversword alliance includes 28 endemic species that represent three genera (*Argyroxiphium, Dubautia,* and *Wilkesia*). A molecular phylogeny has recently been constructed based on nuclear ribosomal DNA sequences. By mapping the distribution of wet versus dry habitat preference onto the phylogenetic tree Baldwin and Robichaux (1995) concluded that there have been at least five independent transitions from ancestors occurring in wet habitats to the derived species occurring in dry habitats. Adaptation to dry habitats in this alliance is known to include morphological and physiological traits that influence leaf energy balance (e.g., leaf dimensions, stomatal conductance, and leaf surface properties that regulate solar reflectance) and physiological traits that influence leaf responses to water stress (e.g., cell wall elasticity and its influence on turgor maintenance) (Robichaux et al., 1990). Unfortunately, the molecular phylogeny exhibited its lowest degree of resolution in those lineages with the greatest physiological diversity, limiting the potential for successful reconstruction of physiological diversification. This illustrates one important constraint on

the process of mapping physiology onto phylogenetic trees, namely that one must have a highly resolved phylogeny before gaining insight into physiological divergence.

Using a similar approach, Todd Dawson (a comparative ecophysiologist) has teamed up with Stephen Weller (a comparative systematist), Warren Wagner (a comparative systematist), and Ann Sakai (a population biologist) to study another group of Hawaiian plants, *Schiedea* and *Alsinidendron* (Caryophyllaceae). They have also observed the wet-to-dry transition in this group (Weller & Sakai, 1990; Weller et al., 1990) and are currently investigating the physiological and ecological attributes (e.g., photosynthetic water-use efficiency, hydraulic properties of the water-conducting system) of these taxa which permit them to exploit the drier habitats. Ultimately, the study is aimed at placing these attributes into a phylogenetic context using character mapping procedures and the current phylogenetic tree (Wagner et al., 1995). This will hopefully provide insight into whether those traits that permit certain species to thrive in dry habitats have arisen through response to selection in their current habitats or are historical artifacts of past selection.

EVOLUTION OF C_4 PHOTOSYNTHESIS

One of the earliest uses of phylogeny to discern evolutionary pattern in a functional plant trait involves C_4 photosynthesis. Within five years after the discovery of C_4 photosynthesis researchers had assembled phylogenetic trees showing the distribution of C_4 plants (Evans, 1971; Moore, 1982). From this effort it was clear that C_4 photosynthesis has multiple origins and represents a derived trait, evolving from the ancestral C_3 photosynthetic pathway (the pentose phosphate pathway).

More recently, Hattersley and Watson (1992) constructed an evolutionary hypothesis in the Poaceae that reflects patterns of C_4 evolution and is consistent with well-accepted, higher-level taxonomic affinities. Extensive reticulation of lineages in the Poaceae makes it difficult to reconstruct phylogeny with high levels of confidence (though monophyly has been established for several subfamilies, see Kellogg & Campbell, 1987). Hattersley and Watson (1992) mapped photosynthetic pathways onto their tentative phylogenetic tree, revealing several possible patterns of C_4 evolution. Of particular importance, it appears that multiple origins of C_4 photosynthesis can occur within a single family and reversals of C_4 photosynthesis, back to the ancestral C_3 type, have occurred in several groups. Such patterns suggest that the evolution and reversal of a pathway involving complex developmental and biochemical modifications occurs with relative ease (see also Watson et al., 1985). This supports decisions of optimization during phylogenetic C_4 mapping in which addition and loss of this pathway are treated as equally likely as two additions. It has been suggested that such labile evolutionary patterns must be founded on a genetic architecture with one, or a few, regulatory genes controlling linked sets of C_4-family structural genes (Watson et al., 1985; Monson, 1989a; Hattersley & Watson, 1992; Ehleringer & Monson, 1993). Thus, relatively few mutations, if they occur in the regulatory genes, can have a large influence on the evolutionary expression of photosynthetic pathway type.

Further work on the evolution of C_4 photosynthesis has been conducted in the genus *Flaveria* (Asteraceae). The monograph by Powell (1978) described 21 species for this genus. Physiological characterization of the component species has revealed that only five or six might be classified as "fully expressed" C_3 or C_4 types (Monson, 1989a; Monson & Moore, 1989). Most of the species reflect some intermediate phenotype between the C_3 and C_4 extremes (the so-called C_3-C_4 intermediates). Some workers have described these C_3-C_4 species as intermediate evolutionary stages on the path from the ancestral C_3 type toward the derived C_4 type (Monson et al., 1984; Monson, 1989a; Brown & Hattersley, 1989). Thus, this appears to be a very active group of species in terms of photosynthetic evolution.

Using the morphological descriptions provided in Powell (1978), I have constructed a phylogenetic tree of this genus (Fig. 5). This tree was used to address the question of whether the appearance of C_3-C_4 intermediate photosynthesis always precedes the appearance of fully expressed C_4 photosynthesis. Support for such a pattern would strengthen the supposition that C_3-C_4 intermediate photosynthesis in this group represents the antecedent to the evolution of C_4 photosynthesis. In this reconstruction, C_4 species were classified as those in which the majority of atmospheric CO_2 is assimilated through the C_4 pathway, and the C_3 and C_4 cycles have evolved coordination to the point where leaves exhibit higher water- and nitrogen-use efficiencies—hallmarks of fully expressed C_4 plants. In this case, improvements in photosynthetic water- and nitrogen-use efficiency were assumed if past gas-exchange measurements have revealed reduced intercellular CO_2 concentrations without reduction in photosynthesis rate below the average expressed by all species in the genus. Such traits are presumably a reflection of the C_4 CO_2-concentrating mecha-

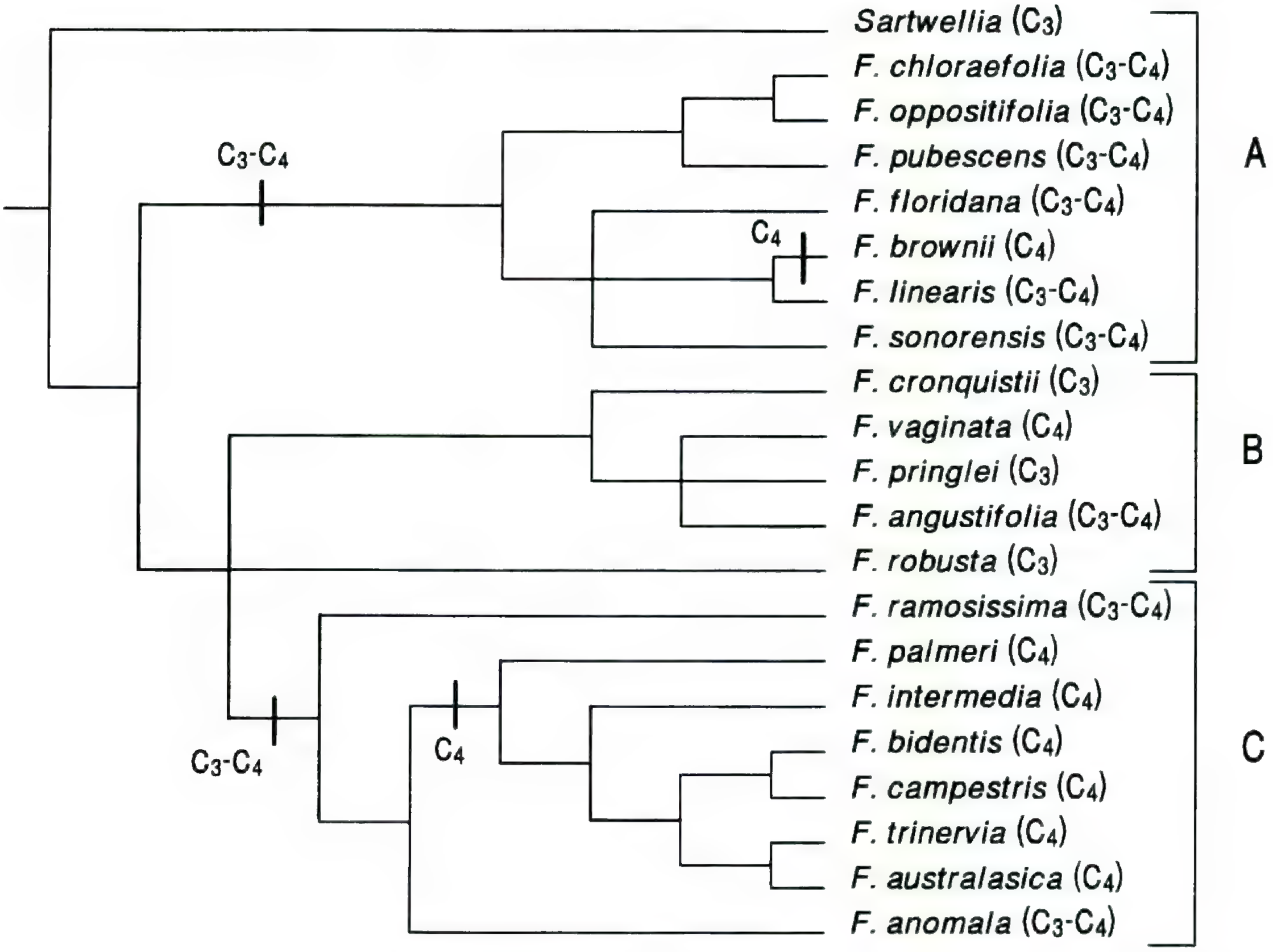

Figure 5. Phylogenetic relationships in the genus *Flaveria* (Flaveriinae–Asteraceae). The tree was constructed using the branch and bound option in PAUP 3.1 (Swofford, 1994). The length of the tree is 33 steps and is characterized by a consistency index (C.I.) = 0.41, a homoplasy index (H.I.) = 0.59, and a retention index (R.I.) = 0.74. All relationships are based on 15 morphological traits that were derived from Powell (1978). Traits included phyllary number, presence or absence of pappus scales, presence or absence of ligules, number of disc florets, presence or absence of discoid heads, length of achenes, density of inflorescence aggregation, presence or absence of self-compatibility, presence or absence of ray florets, overall diameter of the corolla, length of the corolla throat, presence or absence of connate leaves, presence of linear versus ovate leaves, bushy versus erect growth habit, and the presence or absence of leaf spiraling at senescence.

nism. Species with the C_3 pathway are so classified because they exhibit 90% or more of their CO_2 fixation by the C_3 pathway. Species with C_3-C_4 intermediate photosynthesis exhibit considerable CO_2 fixation by the C_4 pathway, but no advantages in terms of elevated water- and nitrogen-use efficiencies. These designations were drawn from past reports of photosynthetic traits in this genus (Ku et al., 1983; Monson et al., 1986, 1987; Moore et al., 1988, 1989; Monson, 1989b; Ku et al., 1991).

The tree exhibits two regions where resolution is such that the sequence of C_3-C_4 and C_4 transitions can be mapped (regions A and C), and one region of inadequate resolution (region B). Using the path of greatest parsimony, the results from regions A and C demonstrate that C_4 photosynthesis has evolved at least twice independently. Additionally, both cases of C_4 evolution were preceded by the appearance of C_3-C_4 intermediate photosynthesis strengthening the hypothesis that this pathway is an evolutionary precursor to fully expressed C_4 photosynthesis. The tree presented in Figure 5 supports evolutionary lability with respect to the C_4 pathway. Within a relatively small group of species there appear to be cases of independent switches among the C_3, C_3-C_4, and C_4 pathways.

Caution should be used in relying too heavily on this tree to identify details of C_4 evolution. The tree is based on a limited number of characters and only yields moderately robust resolution. A tree based on numerous RFLP molecular markers is currently under construction, and is likely to yield greater resolution in interpreting C_4 evolutionary patterns in this group (P. Soltis and M. Ku, unpublished manuscript; M. Ku, Washington State University, pers. comm.). Nonetheless, the example provided

in Figure 5 demonstrates the utility and guidance provided by phylogenetic perspective in the interpretation of metabolic evolutionary patterns.

Concluding Statement

Since Felsenstein's seminal paper (Felsenstein, 1985), comparative physiologists and developmental biologists have observed the birth of a new experimental approach—the rigorous testing of comparative hypotheses using phylogenetic information. The approach is recent in its origins, and there are only a few examples of its successful application. However, the recent publication of several synthetic treatises of the phylogenetic approach and its relationship to comparative biology testify to the growing interest in this discipline (e.g., Huey, 1987; Harvey & Pagel, 1991; Brooks & McLennan, 1991; Lauder et al., 1995). There is no doubt that comparative biologists will come to rely heavily on phylogenetic perspective in future studies. As so aptly stated in Felsenstein's paper: Phylogenies are fundamental to comparative biology. There is no doing it without taking them into account (Felsenstein, 1985).

Systematics and comparative organismic biology will be reciprocally strengthened through the shared use of phylogenetic analysis. Comparative physiologists and developmental biologists will be able to provide a stronger evolutionary interpretation of functional responses to the environment. Systematists will acquire deeper insight into the evolutionary process, as well as help in resolving points of equivocation on phylogenetic trees through the use of new characters. The most pressing limitation to these activities is the availability of adequately resolved phylogenetic maps. The achievement of a successful synthesis will require the continuation of efforts to construct classification systems that (1) deal with groups holding physiological and developmental interest, and (2) are accurate in their reflection of true phylogeny.

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SYSTEMATICS SOLVES PROBLEMS IN AGRICULTURE AND FORESTRY[1]

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ABSTRACT

In forest and agricultural ecosystems the conspicuous elements, namely the trees, crop plants, and farm animals, form complex interactions with many less conspicuous organisms. These less conspicuous but specious organisms such as insects, fungi, nematodes, and bacteria can be beneficial, even essential, or they can be utterly devastating causing billions of dollars damage. Our present knowledge of the systematics of these less conspicuous organisms is limited. For some groups even the most elemental systematic understanding—an inventory, a checklist, a means of identification—is lacking. This paper presents examples in which systematics has contributed to solving a problem in agriculture and forestry. Our current agricultural practices reflect the systematic understanding of pest organisms that influence crop productivity. The success of efforts to discover and develop biological agents that control agricultural pests and pathogens depends on systematics. International exchange of agricultural commmodities can be enhanced or hindered by accurate or inaccurate systematic knowledge as exemplified by the recently opened market for California wheat to the People's Republic of China. Systematics is essential in directing the collection, organization, and use of vascular plant germplasm as for breeding improved crops. Forests in eastern North America have been devastated by the introduction of exotic pests and pathogens. Systematic knowledge helps to prevent such introductions. In Australia native forests threatened with extinction from an introduced weed were saved by the biological control of that weed using a fungus. Detailed systematic knowledge of both the host and pathogen allowed the safe and effective introduction of this biocontrol agent. In all the examples detailed in this paper, basic systematic knowledge was essential to solving important problems in agriculture and forestry.

Trees, crop plants, and farm animals are the most conspicuous elements in forest and agricultural ecosystems, yet these organisms have complex interactions with many less conspicuous organisms. The myriad of insects, fungi, nematodes, and bacteria that are part of these ecosystems can be beneficial, even essential, to the development of the crop, or can be utterly devastating causing billions of dollars damage. At present our knowledge of the systematics of these less conspicuous organisms is grossly limited—so limited that we often do not have even an elemental systematic understanding of their existence—an inventory, a checklist, a means of identification. These are the ecosystems upon which humanity depends for survival.

Within forestry and agriculture there is an increased interest in holistic approaches to managing the biological resources on which these industries depend. Such management strategies must allow the exploitation of biological resources to provide the immediate needs of food and fiber, but also must accommodate management approaches that minimize the impact on the environment and ensure long-term use of these resources. Such strategies include sustainable agriculture, the biological control of pest organisms, integrated pest management, and the management of forests for products other than lumber. Systematic information is the key ingredient in developing these strategies; with adequate systematic knowledge these initiatives can be successful.

This paper presents examples of problems in agriculture and forestry that have been solved by applying a systematic understanding of the organisms involved. In some cases the result was to solve short-term problems with short-term economic gain, for example, in increased international trade, while in other cases the result has been incalculable, long-term benefit, such as in the biological control of an exotic weed that was threatening to destroy an entire ecosystem. In all cases basic systematic knowledge was essential to solving the problem.

AGRICULTURE

AGRICULTURAL PRACTICES REFLECT THE SYSTEMATIC UNDERSTANDING OF PEST ORGANISMS

Agricultural practices of previous centuries included empirically integrated management of crop

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Figure 1. Binucleate hyphae of *Rhizoctonia solani* AG-4 under fluorescence (left) and dark-field microscopy (right). Photo by Marc Cubeta.

pests, often with limited success. During the last 100 years, however, these limitations on agricultural productivity have been lowered, resulting in an increased human population and demand for food. Despite spectacular success, 10–20% of all agricultural crops are still lost to pests and pathogens (Anonymous, 1993). As the need to produce more agricultural commodities increases, expectations have also increased for lower chemical input to agricultural systems and products. Knowledge of the systematics of the insects, fungi, nematodes, and microorganisms that consume a significant portion of the agricultural products provides the key to solving this dilemma.

For example, until recently the fungus commonly identified as *Rhizoctonia solani* Kühn. was believed to be a single, widespread species that occurred on almost every vascular plant and caused root rots, barepatch, wilts, diebacks, blights, and blotches (Farr et al., 1989; Parmeter, 1970). This fungal species produces almost exclusively vegetative hyphae (Fig. 1), albeit vegetative hyphae with distinctive morphology (Parmeter, 1970). In the past 20 years differences were noticed in the rarely formed sexual state, and relatedness was defined on the ability of strains to undergo anastomoses or hyphal fusion. Now the *R. solani* complex is separated into anastomosis groups, or AGs, based on this ability. Recent molecular analyses of the anastomosis groups and increased knowledge of sexual states has allowed systematists to characterize biologically meaningful species that correlate with such important parameters as host susceptibility (Ogoshi, 1987; Sneh et al., 1991). Within the entity previously referred to as *R. solani*, a number of species are now recognized, some of which are pathogens specific to particular crop plants, others are mycorrhizal with orchids, while still others can be used as biological control agents of plant pathogenic fungi (Vilgalys & Cubeta, 1994). This crucial systematic information allows plant pathologists to recognize and seek out control strategies for the species that are pathogenic on specific crops, allows orchid growers to understand the positive aspects of the presence of these fungal species, and allows biological control specialists to use these fungi in their arsenal of control agents. The systematist has made order out of chaos.

SYSTEMATICS PROVIDES THE MEANS FOR DISCOVERING AND DEVELOPING BIOLOGICAL AGENTS TO CONTROL AGRICULTURAL PESTS AND PATHOGENS

Damage to agricultural crops due to fungi, both in the field and during harvest and storage, is estimated at more than $3.5 billion in the United States (Kendrick, 1992), while the dollar value from insect damage is equal or greater. Insects, nematodes, fungi, and microorganisms constantly compete with humans for these commodities. An increasingly attractive alternative to chemical control of agricultural pest organisms is through biological control or the manipulation of a biological antagonist, often a natural enemy. One suspects that considerable biological control exists in natural systems and that the interaction and balance between organisms is extremely complex.

Fungi are being explored as biological control agents of insects, nematodes, plant pathogenic fungi, and noxious weeds. The fungi involved are not the macrofungi with which most people are familiar, that is, mushrooms, polypores, or lichens. Rather, the fungi having the greatest impact in agriculture and forestry are microscopic in size, often fast-growing, and producing many tiny reproductive structures. As a group of organisms they are vastly understudied, to the extent that at least 50% of the new species with biocontrol potential have yet to

be discovered and described. Fundamental systematic information, such as species descriptions and understanding of relationships with known species, is needed.

One example in which systematic knowledge has contributed to the development of effective biological control concerns fungi used to control soilborne fungal diseases in temperate agricultural systems. Like many Ascomycetes, these fungi are most commonly encountered as asexually reproducing strains for which a sexual state may or may not be known. One of the most commonly used biocontrol strains was initially identified as *Gliocladium virens* Giddens, Foster & A. A. Foster. Although described in *Gliocladium*, this biocontrol fungus is morphologically and biologically unlike the type and other species in this genus. Using both morphological and molecular approaches, two systematists have shown that *Gliocladium virens* actually belongs in the relatively unstudied genus *Trichoderma* (Fig. 2) (Rehner & Samuels, 1994; Samuels & Rehner, 1993). Based on that conclusion, one would predict the related sexual state of this fungus would be an ascomycete in the genus *Hypocrea* (Fig. 3). Thus, strains of the closest sexually reproducing relative, *H. gelatinosa* (Tode) Fr., were tested for the production of the fungal metabolite gliotoxin. Gliotoxin is correlated with potential for biological control of fungal pathogens. Strains derived from the closely related sexual state produced as much gliotoxin as the biocontrol fungus. In addition, some of these newly discovered biocontrol strains produced their sexual states in culture, allowing conventional genetic manipulation. Thus, increased knowledge of the systematics of the *Trichoderma* complex led to the prediction and discovery of more effective strains of biological control fungi.

Unlike the above example, agricultural problems are often solved using the brushfire approach of reacting when an emergency arises, undertaking a narrow research program on the pest causing the problem, possibly finding a solution, and going on to the next agricultural brushfire. Because comprehensive systematic knowledge is not generated in solving an immediate problem, the short-term solution does not add significantly to the development of a predictive classification system. In fact, in many situations systematic analysis of a single species, removed from the context of phylogeny and biogeography, and not carefully integrated into a classification system, detracts rather than adds useful information. An example of a circumstance where comprehensive research followed a brushfire solution involved a pest in Africa. An unknown mealybug attacked cassava in West Africa (Fig. 4) and cost farmers £1.4 billion each year (Anonymous, 1986). A systematist described the species (*Phenacoccus manihoti*) as new and, based on the systematic relationship of this species with others, suggested that natural enemy exploration be undertaken in Central and South America (Matile-Ferrero, 1977). Additional specimens of a mealybug erroneously identified as *P. manihoti* were discovered in northern South America, and several of its parasites were imported to Africa. Unfortunately, none of the biological control agents were effective, and a mealybug systematist was asked to study the South American material. The systematist determined that the mealybug from northern South America actually was a second species different from *P. manihoti* described from Africa (Cox & Williams, 1981). Eventually true *P. manihoti* was located further south in South America, and effective parasites were discovered and successfully introduced into West Africa (Herren & Neuenschwander, 1991). After this brushfire was put out, the International Fund for Agricultural Development offered financial support for a study on the mealybugs of South America. A book has recently been published (Williams & Grana de Willink, 1992) that serves as a first step toward understanding the diverse mealybug fauna of the area and prepares the world for the emergence of the next devastating mealybug pest.

INTERNATIONAL EXCHANGE OF AGRICULTURAL COMMODITIES DEPENDS ON ACCURATE SYSTEMATIC INFORMATION

International exchange of agricultural commodities in the United States was valued at $24 billion for imports and $42 billion for exports in 1992, accounting for a significant portion of total domestic exports (Anonymous, 1993). Regulations governing the international exchange of agricultural and forest commodities are directed at the containment of economically damaging organisms. Thus, such exchange requires the accurate and rapid identification of both domestic and exotic pests and pathogens. Systematists provide the expertise and tools on which these identifications are made, allowing the existence of this multibillion dollar industry.

The smut fungi, Ustilaginales, cause severe diseases of important grain crops (Fig. 5). Although relatively well surveyed and described, these obligate parasites are generally considered to be host specific and are identified primarily based on teliospore characteristics. Their identification is difficult and requires taxonomic expertise, particularly

Figure 2. SEM of *Trichoderma virens*, a fungus with potential for the biological control of plant pathogenic fungi. Photo by James Plaskowitz.

if the host is unknown or misidentified. *Tilletia indica* (Mitra) Mundkur, karnal bunt of wheat, is a smut fungus that occurs in limited regions of the world (Green, 1984; Smith et al., 1992; Waller & Mordue, 1983). Extreme vigilance is required to prevent the spread of this pathogen. Recently, wheat (*Triticum aestivum* L.) imported into Canada from the United States was determined to be contaminated with *Tilletia indica*. Plant quarantine officials in both the U.S. and Canada became quite excited, and a ban on the import of wheat from the U.S. to Canada was suggested. A systematist who

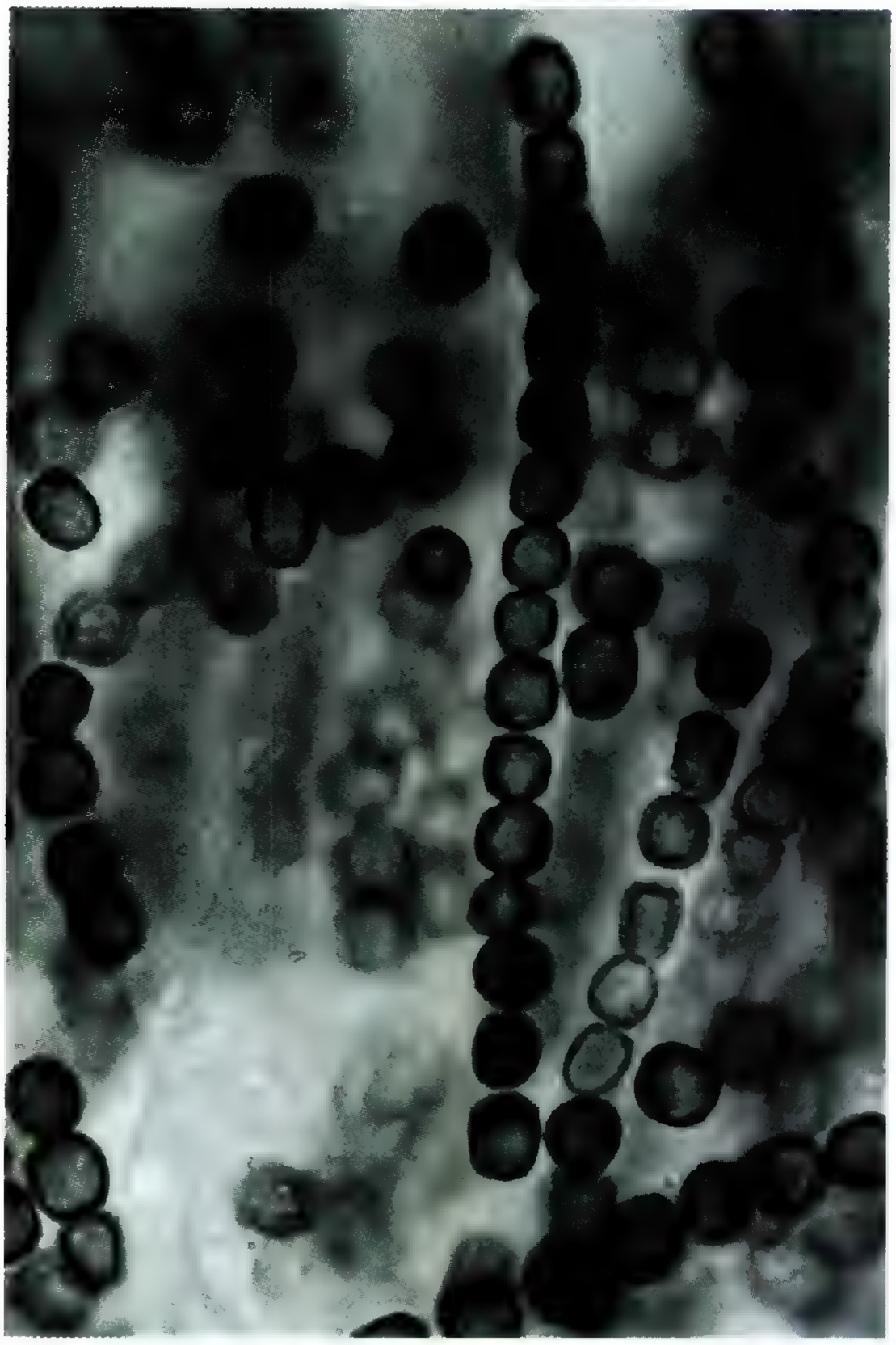

Figure 3. Asci with 16 partspores of *Hypocrea gelatinosa*, the sexual state of *Trichoderma virens*.

Figure 4. Cassava trees in West Africa. The tree on the right attacked by the mealybug *Phenacoccus manihoti* has not produced large, edible tubers, while the one on the left is free of mealybug attack and shows normal tuber production.

was asked to study the material correctly identified the smut as *Tilletia barclayana* (Bref.) Sacc. & Syd. This smut fungus occurs on rice and apparently contaminated the wheat when it was stored in a warehouse that had previously contained rice. This identification was eventually confirmed with isozyme analysis, and a potentially costly international incident was averted (Mary Palm, pers. comm., 1993).

Systematic knowledge of another smut fungus on wheat and the clarification of the circumstances under which it was collected have allowed the sale of wheat from California to the People's Republic of China. Export of wheat from the Pacific Northwest of the United States to the People's Republic of China has been curtailed since 1972 because of the presence of *Tilletia controversa* Kühn., dwarf bunt, a fungus not known to occur in China. A second bunt disease of wheat, common bunt or rough-spored bunt, is caused by *T. tritici* (Bjerk.) Wolff and occurs throughout the world wherever wheat is grown (Anonymous, 1990; Mordue & Waller, 1981). Differentiating teliospores of *T. tritici* from *T. controversa* is difficult to impossible because of their morphological similarity. Thus, it is important to know if dwarf bunt is present, absent, or has ever occurred in specific regions in the U.S. from which wheat might be shipped to the People's Republic of China. The wheat-growing regions of California are free of dwarf bunt except for one report of *T. controversa* (Duran & Fischer, 1956). This report curtailed the export of wheat from California to China. The report of dwarf bunt in California was based on a specimen collected [on June 30, 1917 in Jacksonville, "California"] by a U.S. Department of Agriculture plant pathologist, H. B. Humphrey. The specimen was deposited in the U.S. National Fungus Collections and was available for study. Despite intense efforts using morphological, biochemical, and molecular means, it was not possible to identify this specimen as either *T. tritici* or *T. controversa*. Since identification was not possible, a new strategy was devised that again depended on systematic facilities. All specimen label data associated with the specimens at the U.S. National Fungus Collections had previously been entered

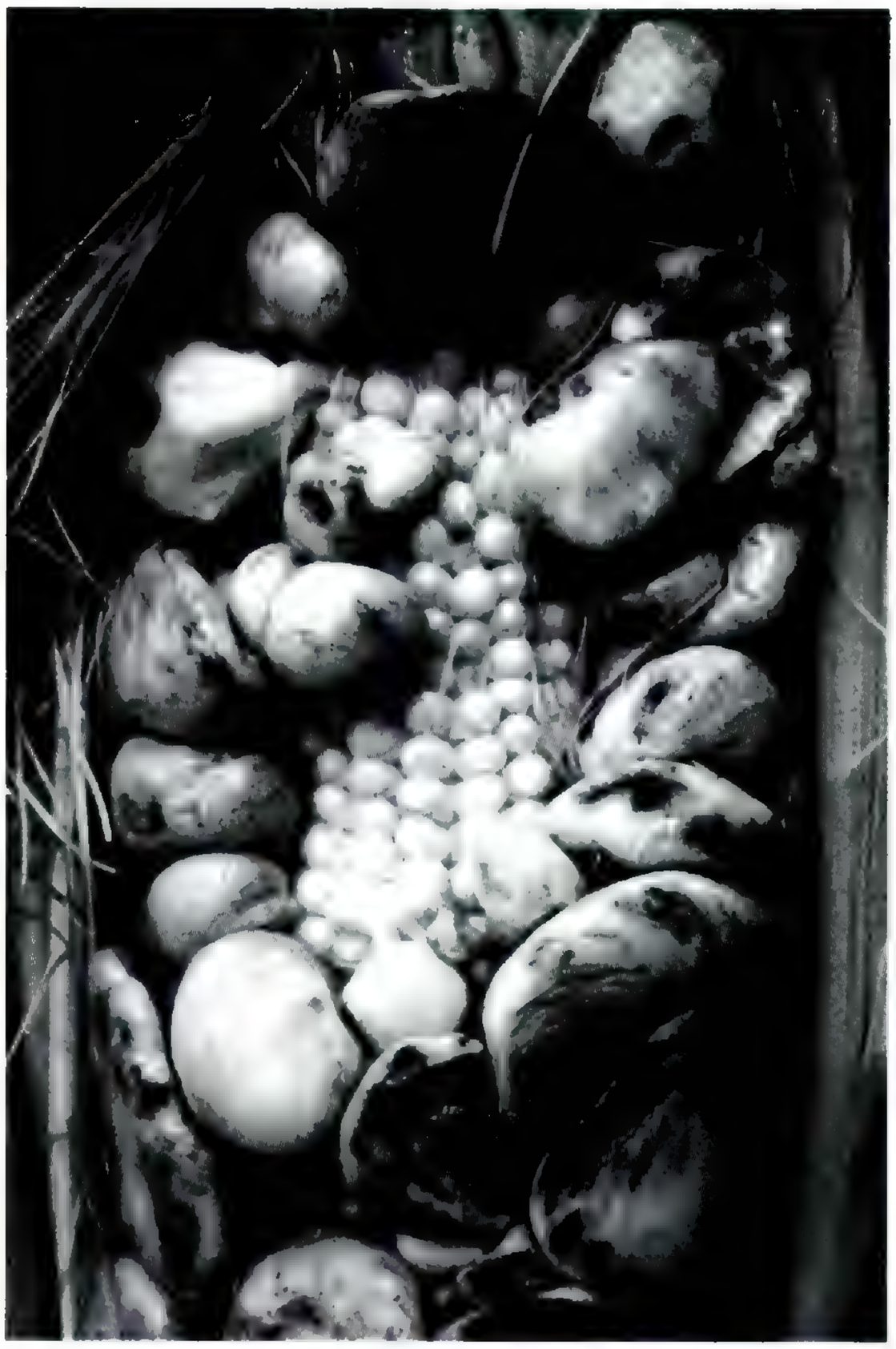

Figure 5. Corn smut fungus, *Ustilago maydis*, infecting kernels of field corn in Maryland.

into a computerized database. Using this systematic information resource, it was possible to determine the approximate route of Humphrey on his 1917 trip (Table 1). Although this database was never intended for tracking a scientific expedition, it provided the information necessary to prove that the dwarf bunt specimen was collected in Jacksonville, Oregon, not in California. This fact was confirmed by the itinerary and telegrams of H. B. Humphrey for this trip deposited and maintained at the U.S. National Archives. Using these sources of information it was proven that this dwarf bunt specimen was not collected in California (Rossman, 1994).

As a consequence, the People's Republic of China has lifted the quarantine on the import of wheat from California. According to the California Wheat Commission (B. Fernandez, pers. comm.), a first shipment of California wheat to the People's Republic of China left Stockton on April 1, 1995. This first shipment of 30,000 tons is worth about $4.7 million. Solving this systematic problem has opened a multimillion dollar market.

SYSTEMATICS DIRECTS THE COLLECTION, ORGANIZATION, AND USE OF VASCULAR PLANT GERMPLASM

Humankind has always assumed that the genetic resources required to support agriculture would continue to exist in nature forever. As an indication of the importance of genetic resource preservation, Congress has recently mandated that the United States Department of Agriculture formulate a program to develop, store, and access genetic resources for all kinds of living organisms (National Research Council, 1991). The report on specifically how this could be done and how much it would cost has been presented to them. This program includes not only vascular plants and animals of obvious importance to agriculture but also fungi, insects, nematodes, and microorganisms. Congress recognizes the essential role that biological diversity plays in human existence. The problem is how to obtain, organize, preserve, and utilize the genetic resources needed to insure that future agricultural needs will be met. The critical basis for developing and utilizing genetic resources is systematic knowledge (Shands & Kirkbride, 1989).

For vascular plant germplasm in the United States, a large system of repositories exists. The U.S. National Plant Germplasm System contains 5–10% of the 250,000 vascular plant species in existence (National Research Council, 1993). Information on the over 400,000 accessions is based on the systematics of the organisms using the Germplasm Resources Information Network. Entry to accession information is through the scientific name of the species, and all communications depend on

Table 1. Route taken by H. B. Humphrey in 1917 as determined by collection data on specimens deposited in the U.S. National Fungus Collections.

Specimens collected by H. B. Humphrey in 1917 deposited in the U.S. National Fungus Collections
• June 24 1917 Campbell, Santa Clare County, California
• June 30 1917 Medford, Oregon
• June 30 1917 Jacksonville, California (actually Oregon)
• July 4 1917 Pullman, Washington
• July 9 1917 St. Paul, Minnesota

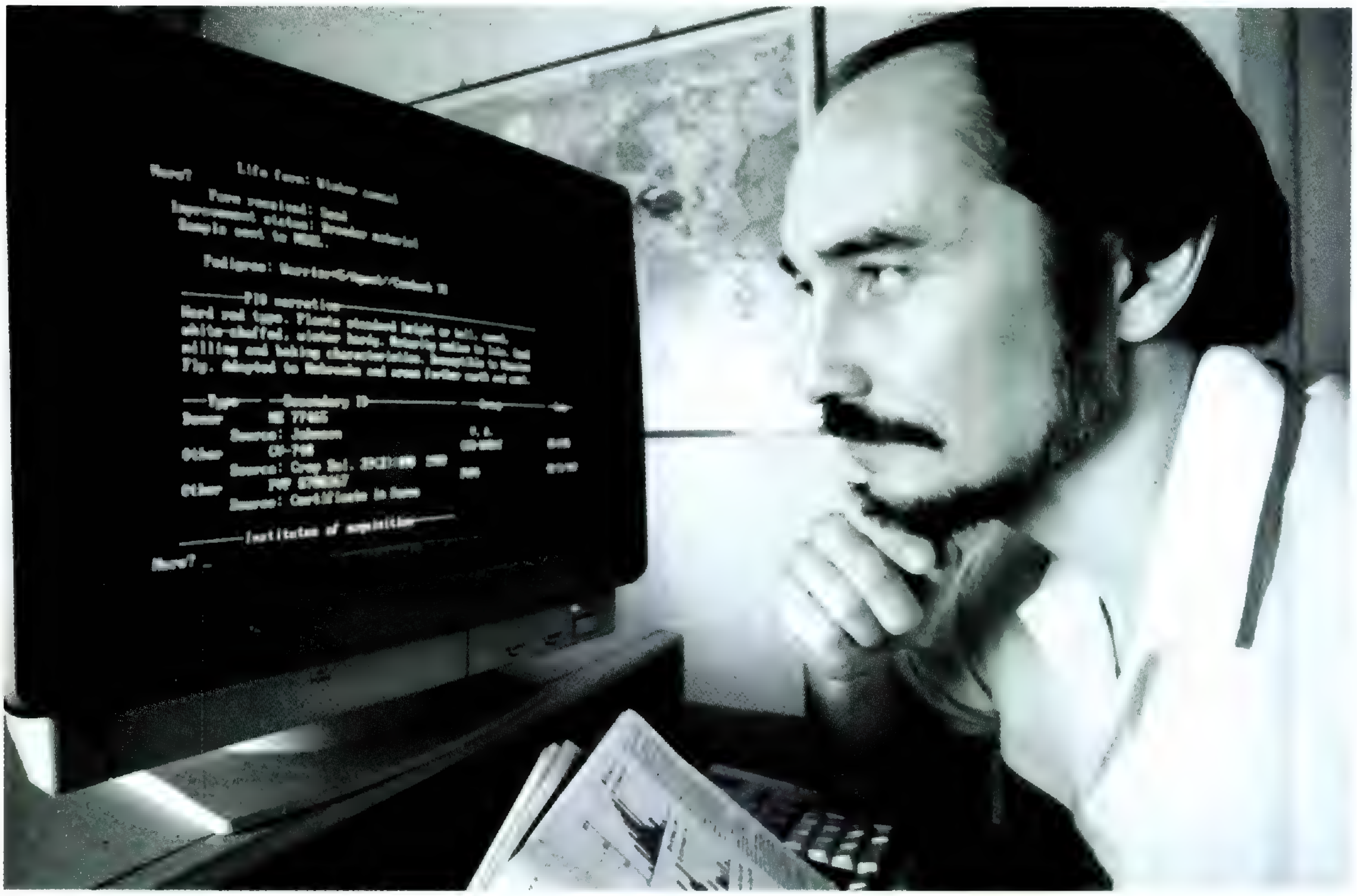

Figure 6. John Wiersema, nomenclaturalist, reviewing scientific names of vascular plants in the Germplasm Resources Information Network.

accurate nomenclature as determined by a systematist specializing in the classification of cultivated plants (Fig. 6). The systematist provides information on the relatedness and therefore the usefulness of the germplasm to its potential crop.

Repositories of vascular plant germplasm set their priorities for collecting and utilizing germplasm based on systematic knowledge of crop plants and their immediate relatives. For example, the numerous wild relatives of the cultivated potato provide the genetic basis for disease resistance that is present in today's crop. Cultivated potato is consumed worldwide and represents the fourth most important food resource (Hawkes, 1990). In the native habitat of wild potatoes ranging from the southwestern United States to south-central Chile, these relatives are often obscure weeds and are not used locally as food; indeed, some are mildly poisonous. David Spooner's research on wild potatoes (*Solanum* sect. *Petota*) illustrates the value of systematics information to plant breeding. Spooner's research has two components—-collecting for more complete germplasm representation in genebanks and systematics research to understand the species and their relationships with *Solanum* sect. *Petota.* His program, collecting in collaboration with researchers from South America, has resulted in the acquisition of more than 20 species—relatives of the cultivated potato—not present in the world's genebanks.

The world's largest collection of potato germplasm at Sturgeon Bay, Wisconsin, holds about 5000 accessions (Bamberg & Spooner, 1994) of about 170 of the 232 wild potato species recognized in the latest comprehensive taxonomic treatment of *Solanum* sect. *Petota* (Hawkes, 1990). At present, there are disagreements among taxonomists regarding the species, hypotheses of natural interspecific hybridization, and the relationships among taxa of cultivated and wild potato. The treatment previous to Hawkes (1990) recognized only 157 species, and the species boundaries and their interrelationships have yet to be reconciled (Spooner & van den Berg, 1992). Thus, Spooner's ongoing research program using a variety of tools to investigate the identity and relationships among these species is crucial for the enhancement of commercial potato products (Giannattasio & Spooner, 1994a, b; Spooner et al., 1993; Spooner & Sytsma, 1992). Because it takes 8–15 years from the initiation of a breeding program to a commercial variety release, considerable time and expense can be saved by making an initial choice of breeding material based on accurate systematic knowledge.

Forestry

Forest land in the United States occupies 737 million acres, yielding products valued at about $1 billion in 1992 (Anonymous, 1993). Other forest commodities and non-commodity uses such as recreation and watershed resources have an even greater value. Changes in the public's perception of the value of forest lands have led to a major shift in their management. This new management philosophy has resulted in older tree stands and in greater value of non-timber species. Long-term forest system management has a different set of problems than those associated with traditional forest management. While most forest managers measure physical and chemical aspects of their forest as well as monitor changes in the macrofauna and flora, they generally are unable to measure the biological diversity of the total forest biota. Knowledge of the systematics of non-timber components of forest ecosystems is essential to their sustainable maintenance.

SYSTEMATIC KNOWLEDGE HELPS PREVENT THE INTRODUCTION OF EXOTIC PESTS AND PATHOGENS THAT DESTROY FORESTS

A major force in the destruction of forests, aside from harvesting of trees, has been damage inflicted by introduced forest pests and pathogens. The economic loss to timber revenues is estimated at $2 billion annually (Campbell & Schlarbaum, 1994), with a much greater loss in recreational value. The infamous American chestnut blight introduced on Asian chestnut nursery stock in 1904 has altered the landscape of the eastern deciduous forest forever (Anagnostakis, 1987). Yet nursery stock and unrefined logs are imported into the United States without thorough knowledge and understanding of the organisms associated with them (Campbell & Schlarbaum, 1994; Redlin, 1991). The fungus causing dogwood anthracnose, *Discula destructiva* Redlin (Fig. 7), was described only recently (Redlin, 1991) but its origin is still unknown because of inadequate baseline data on the fungi in the United States and the rest of the world. Its simultaneous appearance on both coasts of North America suggests that it was introduced on nursery stock (Campbell & Schlarbaum, 1994). Increased systematic knowledge of the inconspicuous organisms that occupy forests worldwide is needed to prevent additional destructive introductions.

Systematic tools for the rapid identification of potentially harmful organisms also will avert future disasters. In 1993 a ship arrived in Wilmington, North Carolina, carrying a cargo of military goods from Germany. When the ship's holds were opened, moths were seen flying from the cargo areas. Agricultural quarantine inspectors closed the holds and set the ship back out to sea. The insects appeared to be the gypsy moth but inspectors were unsure whether they were the European gypsy moth, which is established on the East Coast from an earlier introduction, or the Asian gypsy moth, which does not occur in the U.S. and is notable for its flying females. The samples were shipped to Delaware, Ohio, where systematic specialists used molecular techniques to quickly identify the specimens as the Asian gypsy moth. The ship's cargo areas were fumigated, and a trapping program around the port was initiated to eradicate the Asian gypsy moth before it could become established. Previous development of a rapid identification method by systematists had given quarantine decision makers the tools to avert the establishment of a potentially damaging exotic pest.

Decisions to allow the importation of agricultural and forestry commodities into the United States are generally based on whether a potentially damaging organism already exists in this country. Unfortunately, this assumes that these organisms are known and accurately identified in the U.S. At present only about 50% of the insects (Kosztarab & Schaefer, 1990) and 20–40% of the fungi in the U.S. have been described (Klassen, 1986). A database has been developed of reports of fungi on plants and plant products in the United States (Farr et al., 1989). This database is one of the primary resources on which the Animal and Plant Health Inspection Service depends when making decisions about entry of commodities into the United States. Previously this information was scattered and difficult or impossible for decision makers to obtain. Now with a single source of systematic information, more knowledgeable decisions can be made. In some cases this information has allowed the importation of plant products that previously were prohibited entry because of the lack of knowledge about the organisms in the United States.

Although this database is the most comprehensive account of plant-associated fungi in the world, listing 13,000 species (Farr et al., 1989), it is far from complete, particularly for fungi on non-crop plants. The fungi reported in the literature are usually those that are conspicuous or cause damage to plants of economic interest. We now know that there are potentially pathogenic fungi that live inside apparently healthy plant tissue (Carroll, 1988). Visual inspection of such plants does not detect these latent pathogenic fungal species. As an example of the inadequate knowledge of fungi in the

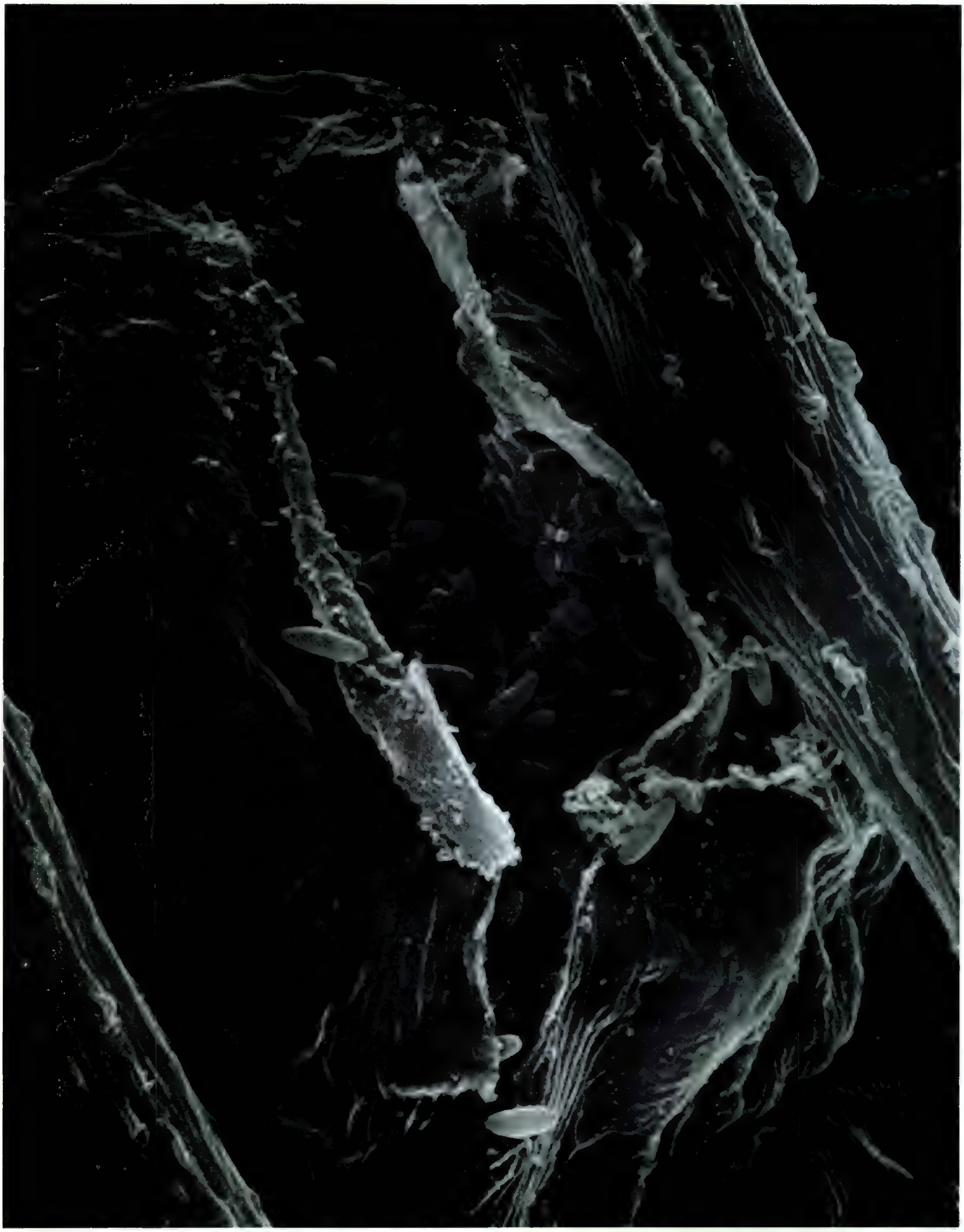

Figure 7. Conidiomata and conidia of fungus causing dogwood anthracnose, *Discula destructiva*, erumpent through leaf epidermis.

U.S., we compared from various sources the fungi known to occur on one host, *Chamaecyparis thyoides* (L.) B.S.P., Atlantic white cedar (Table 2). Although not an inconspicuous host, this tree is not of profound economic importance. In Farr et al. (1989) 40 species are listed on this host. In the U.S. National Fungus Collections, 50 species are represented, of which only 9 are included in Farr

Table 2. Fungi reported on *Chamaecyparis thyoides*, Atlantic white cedar. FOPP (Farr et al., 1989), USNFC (U.S. National Fungus Collections), Bills & Polishook (1992).

Fungi known on *Chamaecyparis thyoides*, Atlantic White Cedar

	FOPP	USNFC	Bills & Polishook
FOPP	40	9	3
USNFC		41	2
Bills & Polishook			72
	40	50	77

Total number of species 153

et al. (1989). Based on these two resources alone, 81 fungal species are known from this host. In just one study Bills & Polishook (1992) isolated 77 fungal species occurring as endophytes in living tissue of this host. Of these, only three species were listed in Farr et al. (1989), while two species were represented in the U.S. National Fungus Collections. From these three resources 153 fungal species are known on *Chamaecyparis thyoides*, of which only 40, or about 25%, are reported in Farr et al. (1989). These data suggest that by simply gathering information from our systematic collections, we can enhance the knowledge base considerably. Then, in this case, by undertaking even cursory sampling activities, we can again double the number of fungal species known from that host. This fundamental knowledge of the organisms that occur in the United States is needed to make enlightened decisions about the safety of allowing entry of agricultural and other plant commodities into this country.

SYSTEMATIC KNOWLEDGE OF HOST AND PATHOGEN IS NEEDED TO CONTROL EXOTIC ORGANISMS

Introduced organisms that threaten forest ecosystems as well as grazing lands can be controlled using biological agents. To be successful, systematic knowledge of both the biocontrol agent and target organisms is critical. For example, in northern Queensland, Australia, a noxious weed known as rubbervine, *Cryptostegia grandiflora* Roxb. ex R. Br. (Asclepiadaceae: Periplocoideae), has ruined grazing lands and threatened the native forests by completely covering the trees. Exotic to Australia, where it was intentionally introduced over a century ago to cover spoils from gold mines, this perennial, woody, climbing shrub still exists in relictual but threatened populations in its native habitat of Madagascar (Evans, 1993). To solve the weed problem in Australia, the native plant populations in Madagascar were examined for both fungus and insect natural enemies. Although insects were located, none were found to be host specific and thus were not considered safe for introduction into Australia.

A rust fungus (Uredinales) with biocontrol potential was collected by Harry C. Evans of the International Institute of Biological Control in 1987–1988. Unfortunately, this rust was considered to belong in the genus *Hemileia* Berk. & Broome, in which is also placed the notorious coffee rust fungus *H. vastatrix* Berk. & Broome. The rust pathogen of rubbervine had been described in 1914 but literally ignored for decades because of its seeming lack of economic importance. Evans (1993) undertook a systematic study of this potential biological control agent and discovered that the nuclear condition of supposed urediniospores was that of a sexually reproducing fungus, thus what appeared to be urediniospores were actually teliospores or the sexual spores of the rust. Under conditions of low humidity, such as occur in the semiarid parts of Madagascar, these prolific urediniospore-like teliospores were produced in abundance. However, with high humidity, such as in a greenhouse in the United Kingdom or as occurs only occasionally in this region of Madagascar, true teliospores are produced that eventually germinate to form a variable number of basidiospores. This rare phenomenon reveals the evolutionary history of this fungus as well as its closer relationship with another group of rusts. This rust is now placed in *Maravalia* Arthur in the Chaconiaceae, Uredinales, only distantly related to *Hemileia*.

Biological control agents must be host specific. In testing for host specificity, close relatives of *Cryptostegia grandiflora* in the Asclepidaceae were examined for susceptibility to the rust fungus. While the target plant proved to be highly susceptible, related species demonstrated a range of resistance that reflected the relationships among the host plants. For example, within the subfamily Periplocoideae of the Asclepiadaceae, the closest related genus, *Gymnanthera* R. Br., proved to be highly resistant with a response that included hyphal collapse after penetration. In another related plant species, *Finlaysonia obovata* Wall., the formation of sori was initiated but pustules did not mature (Evans & Fleureau, 1993). On two species in the subfamily, *Gonocrypta grevei* Baill. and *Cryptolepis grayi* P. I. Forst., fertile sori did develop in greenhouse tests. Further studies on ecotypes of *G. grevei* demonstrated population differences with sporulation on certain plants occurring only at saturation inoculum levels. Based on these findings, two physiological races of the rust fungus were dis-

tinguished, one adapted to *Cryptostegia*, and the other to *Gonocrypta*. This was corroborated by the field observation that rusted *Cryptostegia grandiflora* grew intertwined with healthy *Gonocrypta grevei* (Evans & Tomley, 1994). As a result of increased systematic knowledge of a rust fungus, *Maravalia cryptostegia* (Cummins) Ono, and of the host plant and its relatives, rubbervine in Australia is no longer devastating the forest ecosystem.

This success story is the result of an extremely small piece of the entire systematics puzzle; most pieces of the puzzle remain separated. If there existed a thorough systematic understanding of a majority of the rust fungi, the potential for controlling exotic weeds such as rubbervine would be increased. In some parts of the world exotic weeds threaten the extinction of more biological diversity than the threat of habitat destruction from human activity (U.S. Congress, 1993). Lack of systematic knowledge is hindering use of biological control agents to stop the destruction of endangered native habitats due to exotic weeds. Given the ability of one rust species to control a noxious weed that threatened a native forest in Australia, imagine the untapped potential for the use of fungi as biological control agents. Systematics is the key to achieving that potential.

Conclusion

Many costly problems in agriculture and forestry could be solved with increased systematic knowledge of the inconspicuous organisms that influence forest and agricultural ecosystems. Systematics provides the means to use and benefit, rather than suffer, from their biological influence. The economic payoff from using systematic knowledge to solve problems in agriculture and forestry is far greater than the cost of funding a systematics research program.

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FISHERIES AGENCIES AND MARINE BIODIVERSITY[1]

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Abstract

In addition to the potential negative impacts on biodiversity from fishing activities, there are positive aspects as well. Fisheries agencies are among the best equipped organizations to examine questions involving marine biodiversity because of their long history of studying marine populations. Furthermore, expansion of their involvement in these questions is in the agencies' interest. Fisheries management depends not only on the accurate identification of target species, but also on understanding the ecosystems from which they come. Systematics is the base from which many questions about biodiversity must be addressed. Taxonomy is a critical tool for ecologists. Therefore, in addition to training new systematists, the systematics community must develop better ways to disseminate the information it develops and train other biologists to be proficient in taxonomy. Closer cooperation between fisheries and systematics is urgently needed to develop the knowledge and skills necessary for assessment and maintenance of marine biological diversity.

The problem of conserving biological diversity has received so much attention that almost any scientifically literate person will have heard of it by now. It is rapidly becoming an international conservation priority emphasized in both the scientific (e.g., Harper & Hawksworth, 1994; Eldridge, 1992) and popular (e.g., Sawhill, 1994) press. Governments at all levels in nations around the world are debating and implementing legislative and executive actions to assess and preserve biodiversity. The Convention on Biological Diversity adopted as part of the 1992 United Nations Conference on Environment and Development calls for countries to undertake two major tasks: (1) identify the components of biological diversity that are important for conservation and sustainable use, and (2) integrate biodiversity concerns into socio-economic planning. Institutions that bring together the people who manage, use, and study biodiversity are crucial for achieving long-term responsible management of biological resources.

The widespread debate about what biodiversity is has resulted in a consensus that three levels of diversity are included: genetic diversity within species, phylogenetic diversity (species diversity including consideration of higher-level relationships), and diversity of ecosystems. Debate continues over the relative importance of these components (Barbault & Hochberg, 1992; Brooks et al., 1992; Franklin, 1993; Stiassny, 1992), but degradation at one level affects the other levels as well. For instance, reducing the phylogenetic diversity in model ecosystems alters ecosystem function (Naeen et al., 1994, 1995). This is very important in the context of marine fisheries.

Marine Biodiversity

Consideration of marine and estuarine ecosystems generally has lagged behind terrestrial and freshwater concerns for biodiversity (Norse, 1993; Ray & Grassle, 1991). Aside from early comparisons between tropical rainforests and coral reefs, which are spectacularly diverse and easily visited (Jackson, 1991), marine habitats have remained largely "out of sight and out of mind" at many of the colloquia on biodiversity. This is despite the fact that marine environments occupy 71% of the area and more than 95% of the volume of the biosphere (Angel, 1993). A recent focus on marine biodiversity (e.g., National Research Council, 1995; Vincent & Clarke, 1995) has begun to correct this oversight.

Points made in the many discussions on terrestrial biodiversity cannot simply be extrapolated to the marine environment. The nature of life in the sea is very different from that of terrestrial and freshwater environments (Peterson, 1992; Steele, 1985, 1991). This is especially true in the pelagic (Angel, 1992) and deep-sea (Grassle, 1991) realms. Many more differences in basic body plan, as represented by diversity of phyla, are found in the sea

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than anywhere else (Ray & Grassle, 1991). Life history traits of marine organisms differ greatly from those on land or in fresh waters, particularly with regard to dispersal (Strathmann, 1990). Coastal marine and estuarine ecosystems supply important services to people but suffer from anthropogenic alterations, ironically resulting from the human attraction to the coasts (Ray, 1991).

The difficulty of basic questions about the nature of biological diversity in the sea is increased by our comparative lack of knowledge about marine organisms. Estimates of the number of marine species vary by orders of magnitude (Briggs, 1994; Grassle & Maciolek, 1992; May, 1992, 1994). Population characteristics of marine species are not easily comparable with the better studied examples on land (Palumbi, 1992). Evidence is accumulating for surprisingly high genetic variability of marine populations in currently recognized species such as the common American oyster (Palumbi, 1994) and for the presence of many complexes of morphologically very similar sibling species (Knowlton, 1993), which contrasts with the terrestrial situation. It has been argued that Recent extinctions are not very common in the sea (Culotta, 1994), and conversely, that such extinctions may be commonly occurring but we lack the knowledge to recognize them (Carlton, 1993). Even if there are fewer, widespread species and comparatively few extinctions, it is likely that such a situation increases the importance of each extinction for the health of the ecosystem. Indeed, understanding phylogenetic diversity in marine animals with extensive fossil records, such as foraminifera and mollusks, may allow detailed investigations of the history of life and the processes of diversification (Buzas & Culver, 1991; Jablonski, 1993).

Fishing Effects

Marine fisheries are among the many human activities that impact diversity in marine ecosystems (Messieh et al., 1991). Fisheries, however, specifically target biological resources for harvest. The impact of assorted fisheries varies with the methods employed (Norse, 1993). Whereas some particularly destructive methods, such as dynamite fishing, have been widely prohibited, other methods are a continuing source of controversy. For instance, concerns about the effects of trawling have been voiced for centuries (de Groot, 1984). Of particular concern lately have been bycatch, the incidental mortality of non-target species, and physical disruption of the environment (Kennelly, 1995; Hendrickson & Griffin, 1993). Numerous studies continue to show that these effects vary among habitats (particularly bottom type) and target species (e.g., Hamre, 1994; Riemann & Hoffmann, 1991; Ryan & Moloney, 1988; Van Dolah et al., 1991).

Recently developed fishing methods, such as large drifting pelagic gill nets made of synthetic materials, are controversial (Norse, 1993). The Japanese driftnet fishery for squid began in 1978. By 1986, as many as 36 million "tans" (monofilament gillnet panels 30–50 m long and 7–10 m deep) were being set each year by Japanese vessels (Yatsu et al., 1994a). The Japanese National Research Institute of Far Seas Fisheries estimated that between 1989 and 1991 the bycatch of this fishery included 57,675 cetaceans. Other bycatch of this fishery included millions of blue sharks, albacore and skipjack tuna, pomfrets, and pelagic armorheads, as well as numerous fur seals, seabirds, sea turtles, salmon, and other fishes (Yatsu et al., 1994b). Similar numbers could be expected for the vessels of the Republic of Korea and Taiwan, which comprised a third of the vessels setting driftnets for squid in the North Pacific (Fitzgerald et al., 1994). Reports of this bycatch led to a public outcry to ban the use of pelagic driftnets, known as "walls of death."

The increasing efficiency of harvesting methods, together with increasing numbers of harvesters, often has resulted in precipitous decreases in abundance within populations of target species (Rosenberg et al., 1993). In addition to the obvious economic problems, this can cause profound changes in the ecosystem. For example, in the fishery for bottom fish on Georges Bank (in the Atlantic Ocean east of Massachusetts), 67% of the fish caught in 1963 were the prized gadoids (cod and hakes) and flounders, whereas 24% was made up of unwanted dogfish sharks and skates. By 1986 the dominant catch had shifted dramatically, with 14% gadoids and 74% sharks and skates (Sissenwine & Cohen, 1991). Such changes in populations of large predators could cause profound effects throughout the food web. Similar situations occur in both bottom and pelagic fisheries around the world.

The shift in species fished on Georges Banks is one response to the decreased abundance of some target species. Similarly, fishermen are searching deeper waters for additional species to exploit (Vecchione, 1987), resulting in bycatch and other impacts in new areas. Another response has been development of methods to enhance population size by hatching and releasing the young (Omori et al., 1992). Taking this a difficult step further, some species are reared to harvestable sizes by either ex-

situ aquaculture or in-situ cage or raft culture (Tseng, 1992). Along with problems involving nutrient loading, these culture methods have caused concerns about reduction in genetic variability in the cultured species (Upton, 1992). When exotic species are cultured, the introduction of these alien species (either accidentally or deliberately) into ecosystems (Carlton, 1989) has caused substantial problems with serious ecological and economic results, including reduction in the number of native species (Carlton, 1992).

Fisheries Agencies

A major role of marine fisheries agencies has been to determine why catches of commercial species fluctuate widely. The overall goal has shifted from maximizing catch to achieving sustainable use of the renewable resources (Rosenberg et al., 1993). Many early efforts focused on field surveys of abundance or spawning biomass for data input in single-species population models. The resulting estimates of resource availability have been used with greatly varying success by fisheries managers to determine the amount of catch that can be allowed while maintaining commercially viable populations.

The focus of fisheries management has progressed from single species to multiple target species (e.g., Murawski, 1993) to ecosystems (such as the large marine ecosystem approach of Sherman et al., 1990). For an ecosystem management effort to have any chance of success, information is needed on all abundant or ecologically important species. One aspect that has received particular attention is variability in the recruitment of young stages of commercial species to the fisheries and the interactions of ecosystem dynamics with recruitment (Fogarty et al., 1991; Frank & Leggett, 1994).

Over the years, fisheries agencies have increasingly had to deal with other marine resource issues. In addition to traditional foodfishes, other natural resource products (e.g., aquarium fishes, collectable seashells and coral, etc.) are harvested from the sea, including some with biomedical importance (Wright & McCarthy, 1994). Also, the long history of managing marine populations made fisheries agencies the organizations of choice for protecting threatened and endangered species (Upton, 1992), as well as insulating the species from fishing activities. In some countries, the agencies participate in the design and management of marine parks and other natural reserves. Along with the parks and the endangered species responsibilities, fisheries agencies become involved in regulating non-consumptive uses of living marine resources, such as whale watching off New England. Efforts to preserve ecosystem integrity and to protect coastal nursery areas have moved the agencies into the broad field of environmental protection and pollution abatement. This in turn has forced the inclusion of pollution indicator species (Parker, 1991) into fisheries concerns.

Often during difficult economic times, people try to supplement or replace lost income by harvesting natural resources (e.g., Vecchione, 1987). Also, changes in strategies for managing fisheries resources can cause widespread direct and indirect effects on the economics of coastal communities (Smith, 1995). One of the most difficult aspects of implementing new regulations is the resistance to changes in traditional fishing methods. Thus, human cultural implications have had to be considered in addition to attempting to manage the harvest (e.g., Smith, 1994).

These complex tasks have required the development of an extensive data-collection infrastructure in addition to ongoing resource surveys. Many databases exist that contain vast detailed information about changes in abundance of many fish, crustacean, and cephalopod populations and their genetic variability. Furthermore, many specimens have been deposited in archival museums (Collette & Vecchione, 1995). This combination of data and specimens is particularly important because historical data can be found for comparisons with present or future conditions (Allmon, 1994; Tyler, 1994).

Collette and Vecchione (1995) recently summarized the importance of systematics and taxonomy in fisheries. Many workshops and study panels have pointed to an upcoming crisis in the systematics of marine invertebrates (Winston, 1992). There is a lack of replacements for current research positions at the Smithsonian Institution and other major museums around the world for many groups of marine invertebrates (Feldmann & Manning, 1992). Over a two-decade period (1976–1995), the number of fish specimens in collections in the United States and Canada increased by 77%, while over the same period the number of curators/researchers responsible for those collections decreased by 73% (Poss & Collette, 1995). A major reason for this worldwide decline has been a continuing decrease in funding, prestige, and number of positions in systematics (Cotterill, 1995). There is a need to train additional systematists for placement in an increased number of positions, both in fisheries agencies and in the scientific community at large, so that experts are retained for every important group of organisms. In addition to training additional sys-

tematists, the systematics community must find better ways to disseminate knowledge of their groups and train fishery biologists, ecologists, and others to use up-to-date taxonomy as a tool in their research. Resource management agencies should hire systematists to provide the agencies with needed expertise and to bear a share of the costs of funding systematics.

Fisheries agencies that already are surveying for other fisheries-related problems could easily and with little added effort or expense expand those surveys to focus on questions of biodiversity. Coordinating these activities with museums and academia would allow maximum return while minimizing duplication of effort (Hoagland, 1994).

Proposed Actions

Some proposals made to the U.S. National Oceanic and Atmospheric Administration (NOAA) are listed below as an example of how a federal agency can expand its efforts in marine biodiversity. We feel that these proposals could be applied to fisheries agencies worldwide with only minor adjustments (Fig. 1).

1. Develop Information Systems for Biodiversity Metadata

Fisheries agencies have databases on the distribution of most economically important organisms and some other species that live within their respective geographic area, in addition to concurrent environmental parameters. Museums are computerizing information on the specimens in their collections. Furthermore, visual information (e.g., videotapes recorded by submersibles) has been archived and could be used to document biodiversity that was observed in areas difficult to sample conventionally (Felley & Vecchione, 1995). All of the data mentioned above can be accessed by metadata to form a marine biodiversity database that can address questions such as whether there have been changes in marine biodiversity similar to those reported in terrestrial and freshwater ecosystems.

Biodiversity metadatabases can be constructed from minimal data: species name, locality, depth, date, and either catalog or station number to refer back to the original complete records. Accuracy of species identification and linkage to voucher specimens deposited in archival museums are vital to insuring taxonomic credibility of the databases. Such databases can provide a current and retrospective picture of biodiversity to detect any changes that are occurring. Biodiversity databases will reduce duplication of collecting efforts in carrying out marine biological inventories. Properly constructed, these databases can be integrated with other national efforts to catalog biological diversity, including all biomes (e.g., the U.S. National Biological Survey and the proposed National Biodiversity Information Center). Such efforts are already well under way in Australia, Mexico, and Costa Rica.

2. Expand Existing Sampling and Monitoring Programs

Most fisheries agencies conduct field surveys to provide information for resource management. The major cost of marine sampling is putting a research vessel to sea. The cost of preserving a broad taxonomic suite of material for the study of diversity is comparatively much less. A team of taxonomic specialists and field technicians should be added to fisheries laboratories currently carrying out resource surveys. These personnel could be employed directly by the agencies or under contract from universities, etc. They would be charged with sampling a broad array of organisms, not just those of economic importance. They would utilize additional types of gear and, if necessary, special techniques to preserve specimens. They would facilitate the flow of well-preserved voucher specimens to systematic specialists at universities and museums, and study part of the material themselves.

3. Define Detailed Questions and Develop Methods to Assess and Manage Biodiversity

Detailed achievable goals have not yet been defined for assessing and managing marine biodiversity. One such question currently being posed is whether an all-taxon survey of a marine area is feasible. A demonstration project, limited in time and area, should be established to identify specific research and management goals and capabilities for long-term information and conservation needs. This project would involve specific sites of contrasting characteristics to define attainable goals, which then could be expanded as necessary throughout the nation's waters.

4. Inventory Sanctuaries and Reserves

Sanctuaries and reserves often have been established based on politics rather than biology. Boundaries have been drawn based on governmental jurisdiction instead of knowledge about the life histories of resident organisms. Existing biodiversity in these areas cannot be maintained without

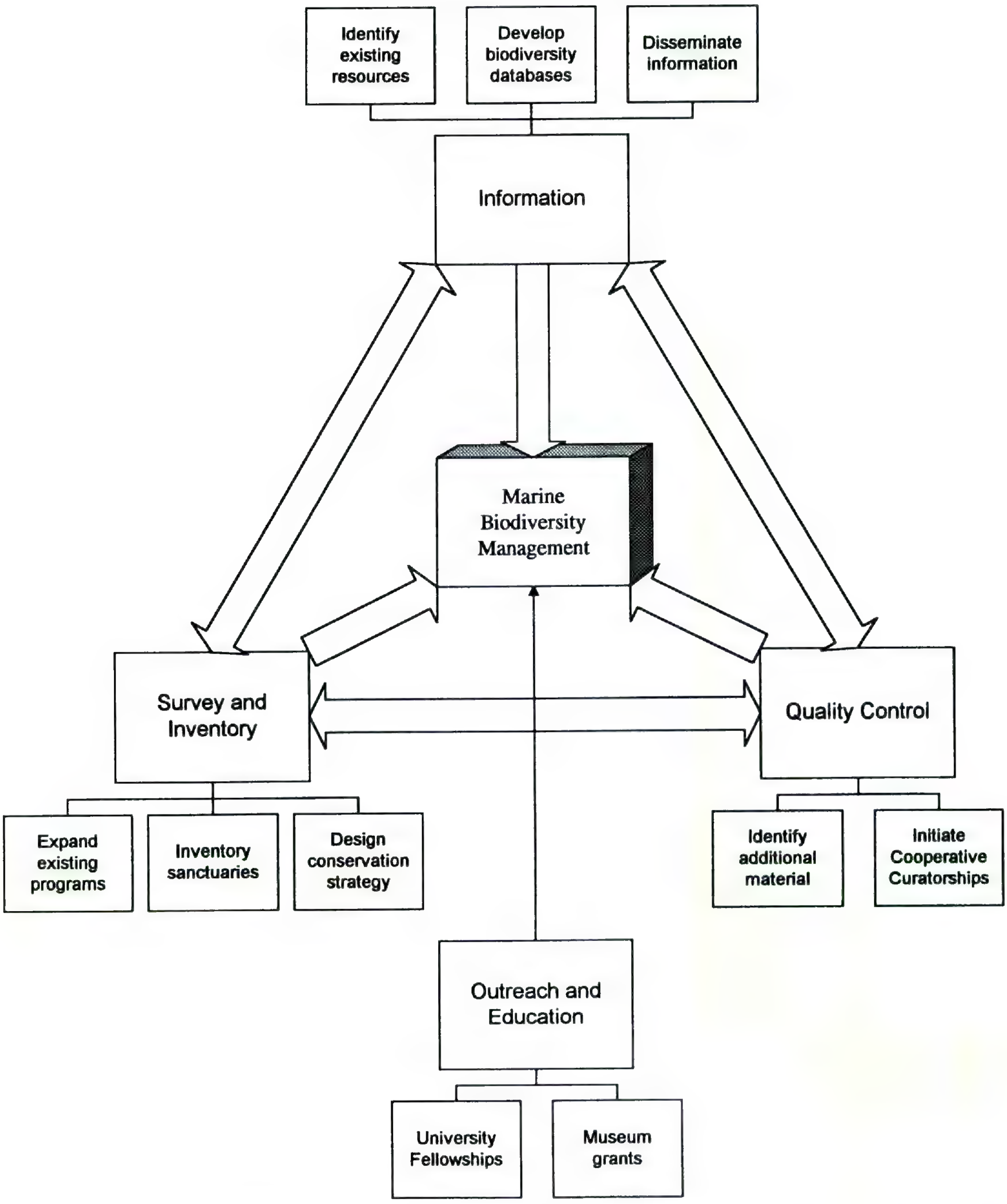

Figure 1. The 10 actions proposed for fisheries agencies in the text, and how they fit into a plan to assess and maintain marine biological diversity.

knowing what species live in each. In order to manage these areas, their species composition and abundance must be inventoried. This task has two components. First, any existing information on the biota of each sanctuary and reserve should be synthesized. Second, these syntheses should be supplemented by additional collecting from ships and in-situ observations. Voucher specimens documenting the occurrence of different kinds of organisms in the sanctuaries should be deposited at nearby

museums. After this, life-history information is needed to determine whether populations are self-sustaining within the boundaries of the sanctuary or if modification of the boundaries is necessary to maintain populations of key species.

5. STUDY ADDITIONAL MATERIAL COLLECTED OR ARRANGE FOR ITS STUDY

Much new material will be collected by the fieldwork described above and will need to be identified. This will require an increased number of specialists in the taxonomy of groups of marine organisms that now lack adequate systematic experts. Specialists need to be added to museums to study poorly known speciose groups of marine invertebrates, such as small bivalves and gastropods, sponges, cnidarians, cumaceans, organisms parasitic on fishes, various groups of worms, and microorganisms. Such specialists are vital to assure the accuracy of identifications. Furthermore, a relatively small number of specialists will then be available to train other biologists in taxonomy as needed. In order for systematics to attract students, more positions and funding must be made available.

6. DEVELOP A PROGRAM OF COOPERATIVE SYSTEMATICS CURATORSHIPS

Insure that at least one expert exists for every major group of organisms by setting up a system of cooperative curatorships in museums holding major collections of marine specimens. These systematists would be hired or contracted by fisheries agencies with consultation of the museums in which they are located, similar to the National Systematics Laboratory at the U.S. National Museum of Natural History. Agencies should insure that there are positions available for the systematists they train to identify organisms, write keys, study phylogeny, and produce monographs. Taxonomic credibility must be maintained for the biodiversity program to be effective.

7. HELP FUND MUSEUMS HOLDING LARGE COLLECTIONS OF MARINE SPECIMENS

Good collections must be maintained to avoid expensive repeat sampling. Information from a large number of such collections is needed to create marine biodiversity databases. Cooperation with museums is vital to the success of a marine biodiversity program because museums hold most of the collections of marine organisms that serve as vouchers for species occurrence and employ most of the limited expertise available to identify many groups of marine organisms. Most museums are currently understaffed at all levels, so the necessary information will not become available for a long time unless these institutions receive assistance. Such funds could also be used to facilitate the incorporation of important collections maintained by individual investigators at universities, marine stations, and fisheries laboratories, into archival museums so that the information can become part of the museum databases.

8. DEVELOP FELLOWSHIPS IN SYSTEMATICS

Training additional marine systematists can be accomplished by developing a fellowship program to support students in cooperating graduate schools, similar to the U.S. Fish and Wildlife Service's Cooperative Research Program and NOAA's Cooperative Marine Education and Research programs (CMER) at several northeastern U.S. universities. Some universities will be associated with museums housing Cooperative Systematics Curatorships. These fellowships could provide additional training to current fisheries employees to fill some of the new positions described above.

9. DESIGN NEW WAYS TO DISSEMINATE TAXONOMIC INFORMATION

New ways are needed to transfer information on taxonomy to a wide array of user groups and to simplify learning of a taxonomic discipline. Novel tools include multimedia computer keys to facilitate identification of marine biota by fishery biologists on shipboard, and fisheries agents collecting statistical information at landing ports. Computerized information could be distributed via the Internet or on CD-ROM. These systems could best be designed in cooperation with ongoing project development such as that at the Smithsonian Institution and the Institute of Taxonomic Zoology at the University of Amsterdam.

10. PUBLISH MARINE BIODIVERSITY RESEARCH

An outlet is needed for monographs related to marine biodiversity such as taxonomic revisions and the series of larval fish guides being produced by fisheries laboratories (e.g., Matarese et al., 1989). Credible lists of species identifications and abundances in local ecosystems should be published either electronically or in journal format. Along with this, a marine biodiversity newsletter could be produced electronically for rapid dissemination of informal information.

What Are the Benefits?

A successful marine biodiversity program will produce information that will assist in managing living marine resources and assuring that representative segments of the biota that inhabit the ocean today will be here for our children to appreciate. Fisheries agencies should take the lead in marine biodiversity research and conservation. An additional benefit of a formal biodiversity program would be to demonstrate a pro-active position for fisheries agencies in understanding marine ecosystems for their future protection.

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IMPORTANCE OF SYSTEMATICS TO PUBLIC HEALTH: TICKS, MICROBES, AND DISEASE[1]

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ABSTRACT

Ticks are vectors of nematodes, protozoa, rickettsiae, spirochetes, other bacteria, and viruses that cause disease in humans and other animals. Complex relationships have evolved between particular tick species, certain organisms that they harbor and transmit, and susceptible vertebrate host species. Effects of tick-borne organisms on host species vary from asymptomatic to fatal depending on the species involved and their interactions. It is critical that arthropod vectors and the organisms they transmit be identified accurately. Unfortunately, there is a crisis in biosystematics of arthropods due to several factors noted in the introduction. Approximately 80 of the estimated 850 described tick species occur in the United States; although all feed on vertebrate blood, only a relatively small number impact people and livestock directly. These few species, however, are responsible for considerable illness and economic loss. Tick-borne Lyme borreliosis is prevalent in North America, Europe, and Asia. It accounts for more than 90% of all reported vector-borne disease in the United States. Totals of 9,677, 8,185, and 11,424 cases were reported for 1992, 1993, and 1994, respectively, by the Centers for Disease Control and Prevention. An overview of interactions among tick species, tick-borne microorganisms, and hosts is provided, with major emphasis devoted to ticks of the *Ixodes ricinus* species complex and the Lyme disease spirochete *Borrelia burgdorferi* sensu lato. Systematics play a crucial role in understanding these interactions.

Complex and fascinating relationships have evolved between particular tick species, certain organisms that they harbor and may transmit, and susceptible vertebrate host species. The effects of tick-borne organisms on host species vary from asymptomatic to fatal depending on the species involved.

For obvious reasons, it is necessary to recognize tick species and the organisms they harbor before a rational plan can be developed for tick control or prevention of disease. Likewise, if a tick bite has occurred, the clinician needs to know whether and how to treat the patient. Identification of tick species is crucial to both decisions. Identification of the transmitted organism is also desirable prior to attempts at intervention, and this may involve complicated taxonomic considerations. The science of systematics, therefore, forms one of the foundations of public health, veterinary medicine, and agriculture. Regrettably, there is a crisis in biosystematics of arthropods, especially those of medical and veterinary importance (Oliver, 1988).

The deterioration of biosystematics capacity is due to several reasons, including decreasing numbers of specialists competent to carry out the needed tasks. Difficulties are exacerbated due to poor financial support. The advanced age of many scientists involved in biosystematic research and lack of new specialists being trained in this area suggest that the condition will worsen unless attention is focused on this problem. A recent report titled, "Endangered Species: Doctoral Students in Systematic Entomology" (Daly, 1995) indicates there were 111 such students in 1992 in the United States and Canada, down from 155 in 1982. Forty percent of the departments surveyed that have insect systematists on their faculties have no doctoral students in insect systematics. If the 28% drop recorded between 1982 and 1992 is extrapolated, the number of such students might reach zero by 2017. These facts do not bode well for a world experiencing new and reemerging arthropod-transmitted and other diseases. If the trend of neglecting systematics research and training continues, it will cripple the Consortium Systematics Agenda 2000 goal to discover, describe, and classify the world's species. It

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will also devastate the newly created United States National Biological Service. Clearly, there is a practical and immediate need for expertise in systematics.

Ticks are obligate blood feeders in one or more active stages of their development. They serve as vectors (transmitters) of nematodes, protozoa, rickettsiae, spirochetes, other bacteria, and viruses that may cause disease in humans and other animals. In addition to serving as vectors of the above-mentioned organisms, they may also cause severe problems to hosts simply by feeding on them. Feeding results in blood loss and produces a puncture wound that can itself become secondarily infected. Injections of tick saliva from some species cause an immediate and/or delayed hypersensitivity. Strains of some tick species secrete a toxin that causes an ascending paralysis (tick paralysis) in their hosts that previously was confused with symptoms due to polio. Clearly, ticks are a global medical and veterinary problem causing severe host reactions and large economic losses under certain circumstances. However, only about 10% of the approximately 850 described species impact humans and livestock directly. Approximately 80 species occur in the United States. Some species are host specific, with all developmental stages (larvae, nymphs, adults) feeding primarily on one host species (e.g., *Boophilus microplus* (Canestrini) feeds on cattle), whereas other species (e.g., *Ixodes scapularis* (Say)) may feed on at least 119 different species of reptiles, birds, and mammals (Anderson & Magnarelli, 1994).

The eight major tick-borne diseases that infect humans in the United States today are Lyme disease, relapsing fever, tularemia, Rocky Mountain spotted fever, ehrlichiosis, babesiosis, Colorado tick fever, and tick paralysis (Spach et al., 1993). Of these, Lyme disease (Lyme borreliosis) is most prevalent in North America, accounting for more than 90% of all reported vector-borne diseases, including those vectored by mosquitoes, fleas, etc. Totals of 9,677, 8,185, and 11,424 cases were reported for 1992, 1993, and 1994, respectively, by the Centers for Disease Control and Prevention (CDC) (1994, 1995). Because of the impact of Lyme disease (LD) in North America, Europe, and Asia, this disease has been chosen as an example to illustrate the importance of systematics to public health. Emphasis will focus on the fascinating interactions among vector tick species, the etiologic agent (spirochete) causing LD, and reservoir hosts of the etiologic agent. Inter- and intraspecific differences among tick vectors, among the causative spirochete species, and among vertebrates serving as tick and spirochete hosts are presented in relation to enzootic cycles in nature and human LD. Prior to discussing these relationships, however, it is necessary to provide a brief background on LD to allow a better understanding of variations and interactions that will be emphasized.

Lyme Disease

Lyme disease is maintained in an enzootic cycle in nature. The cycle involves spirochetes as the etiologic or causative agent, rodents as the most common, but not exclusive, reservoir hosts for the spirochetes, and ticks as the vectors of the spirochetes among the rodents or other animals. Humans are incidental to the natural cycle and are not involved in its maintenance.

SYMPTOMS

Lyme disease (LD) is a multi-systemic illness in humans. Early symptoms include an annular erythematous expanding skin lesion called erythema migrans (EM). It generally clears in the center and is often called a "bull's-eye" rash. Approximately 60% of patients present an EM rash, which occurs days to weeks after infection. Other early symptoms may occur with or without EM and include severe headache, extreme fatigue, joint pains, muscle pain, low-grade fever, swollen lymph glands, stiff neck, keratitis of the eyes, and a general feeling of body discomfort. These symptoms may or may not be followed by neurologic or cardiac symptoms and migrating attacks of arthritis (including pain and swelling) especially in the large joints. The neurologic complications include facial palsy, headaches, difficulty concentrating or sleeping, irritability, and poor motor coordination. Cardiac problems often include irregular heartbeat and varying degrees of heart block that may cause dizziness. Late or chronic stage LD often occurs months to years after infection and usually involves chronic arthritis and/or chronic neurologic effects. Clinical symptoms vary from patient to patient. Arthritis caused by Lyme disease is less common in Europe than the United States, but neurologic complications are more prevalent in Europe as is another LD skin manifestation, acrodermatitis chronica atrophicans.

ETIOLOGIC AGENTS

Lyme disease is caused by the spirochete *Borrelia burgdorferi* sensu lato. Spirochetes are a group of motile gram negative spiral-shaped bacteria in the order Spirochaetales, which includes two families: Spirochaetaceae and Leptospiraceae. The

Table 1. Several examples of spirochetal infections.[a]

Spirochete	Human disease	Vector or source of infection
Borrelia		
B. burgdorferi	Lyme disease	Ixodid ticks
B. recurrentis	Epidemic (louse-borne) relapsing fever	Body louse, *Pediculus humanus humanus*
B. hermsii		
B. turicatae	Endemic (tick-borne) relapsing fever	*Ornithodoros* spp. ticks
B. parkeri		
Leptospira		
Leptospira interogans	Leptospirosis (Weil's disease)	Exposure to contaminated animal urine
Treponema		
Treponema pallidum subspecies (subsp.) *pallidum*	Syphilis	Sexual contact, transplacental
T. pallidum subsp. *endemicum*	Bejel (endemic syphilis)	Direct contact with contaminated eating utensils
T. pallidum subsp. *pertenue*	Yaws	Direct contact with infected skin lesions
T. pallidum carateum	Pinta	Direct contact with infected skin lesions

[a] Slightly modified from Pavia (1994).

genera *Borrelia*, *Leptospira*, and *Treponema* are members of these families and contain species that cause several diseases of humans (Table 1) (Pavia, 1994). The pathogenic spirochetes are long, up to 50 μm, but very thin in diameter and exhibit a spiral, helical shape. They have a relatively slow rate of growth: 20- to 33-hour division time compared to *Escherichia coli*'s 20 minutes. Most pathogenic spirochetes (*Borrelia*, *Treponema*) are microaerophilic and were once thought to be anaerobes (Pavia, 1994). *Borrelia burgdorferi* has linear plasmids that code for outer-surface proteins. The spirochetes are extremely sensitive to elevated temperatures (≥38°C).

Originally, Lyme disease in the United States and Europe was thought to be caused by the same *Borrelia burgdorferi* strain that was isolated in New York by Burgdorfer et al. (1982) and described by Johnson et al. (1984). Data now indicate that the etiologic agent of human Lyme disease worldwide is best recognized as *B. burgdorferi* sensu lato, comprised of *B. burgdorferi* sensu stricto (Johnson et al., 1984; Baranton et al., 1992), *Borrelia garinii* (Baranton et al., 1992), and *Borrelia afzelii* (Canica et al., 1993). All three "genospecies" occur in Europe and cause human LD. Only *B. burgdorferi* sensu stricto has thus far been reported to cause LD in the United States. *Borrelia japonica* found in Japan is currently considered to be the fourth "genospecies" in the *B. burgdorferi* sensu lato complex, but its association with human disease is presently unknown (Kawabata et al., 1993).

TICK VECTORS

Borrelia burgdorferi is transmitted to humans by ticks in the *Ixodes ricinus* species complex. The main species responsible for infecting humans with LD in the United States are *I. pacificus* in the far west and *I. scapularis* in the central and eastern United States. In Europe, *I. ricinus* is the principal vector, as is *I. persulcatus* in parts of eastern Europe eastward to Japan. There are areas of geographic overlap of *I. ricinus* and *I. persulcatus* in eastern Europe and western Russia. The previously mentioned four most common vector species are opportunistic, feeding on various species of reptiles, birds, and mammals. Some of the most common hosts of larvae and nymphs, such as the mouse *Peromyscus leucopus* in the northeastern U.S., also serve as excellent reservoirs for *B. burgdorferi*; whereas others, such as deer, supply a blood meal to large numbers of adult ticks, but apparently may play only a minor role (Oliver et al., 1992) or no role as reservoirs for the spirochete (Telford et al., 1988).

There are ten other less common tick species worldwide assigned to the *I. ricinus* species com-

plex (Keirans et al., 1996a), and their vector status is unknown. *Borrelia burgdorferi* sensu lato also has been isolated from other *Ixodes* species not considered taxonomically to be part of the *I. ricinus* complex, and some of these ticks are involved in several different enzootic cycles of *B. burgdorferi* in nature. Some of these enzootic cycles may impact humans indirectly by providing a source of infective spirochetes. For example, in California *B. burgdorferi* is maintained in a natural enzootic cycle in the dusky-footed woodrat *Neotoma fuscipes* by the maintenance vector *I. neotomae*. *Ixodes neotomae* does not usually feed on humans, but *I. pacificus* feeds on humans and woodrats and thus serves as a bridge vector (Brown & Lane, 1992).

Most of the data available on Lyme disease in the United States originate from research conducted in the hyperendemic northeastern region, where the white-footed mouse *Peromyscus leucopus* is the principal reservoir host for the spirochete and *Ixodes scapularis* is the main tick vector (see Lane et al., 1991, for review).

Variation and Heterogeneity of *I. scapularis*

Ixodes scapularis is extremely important from a public health and veterinary medicine perspective. It is the tick vector involved in most Lyme disease and human babesiosis cases in the United States. There has been controversy regarding its specificity for many years and this has intensified during the last decade. It provides a dramatic example of the importance of systematics to human welfare. When northern populations of *I. scapularis* were described as a separate species (*I. dammini*) and identified as the main vector of the Lyme disease spirochete (*B. burgdorferi*), there was a question as to the efficiency of *I. scapularis* (southern populations) to transmit the spirochete. The perceived absence of *I. dammini* (northern populations of *I. scapularis*) in the south was one of the reasons cited that Lyme disease occurred there rarely, if at all. Subsequently, laboratory experiments demonstrated that southern populations were also vector competent (Piesman & Sinsky, 1988; Mather & Mather, 1990). Later, when southern populations from nature were examined, specimens were found infected with *B. burgdorferi* (Oliver et al., 1993a). Because Lyme disease is so important, it justifies a fuller account and also serves as an example of the importance of systematics to public health.

A complete taxonomic history of *I. scapularis* is provided by Keirans et al. (1996b). Briefly, *Ixodes* (*Ixodes*) *scapularis* was described by Say (1821); however, subsequently several tick experts considered it a variety or a subspecies of *Ixodes ricinus* (Nuttall & Warburton, 1911; Schulze, 1939). Later authors accepted *I. scapularis* as a species and Cooley & Kohls (1945) redescribed it. Since that time it was accepted as a species (Keirans, 1982, 1985). There appeared to be general agreement about the taxonomic status of *I. scapularis* for more than three decades, until 1979. At that time, a new species (*I. dammini*) was described (Spielman et al., 1979) based on populations of *I. scapularis* from the northeastern United States.

Since the description of *I. dammini*, there has been disagreement regarding its status as a separate species distinct from *I. scapularis*. Recently, it was determined to be conspecific with *I. scapularis* (Oliver et al., 1993b); and, since the name *Ixodes scapularis* (Say), 1821, had priority over the name *Ixodes dammini* Spielman, Clifford, Piesman & Corwin, 1979, *I. dammini* was relegated to a junior subjective synonym of *I. scapularis* (based on Article 23 of the *International Code of Zoological Nomenclature*, Ride et al., 1985). Data supporting conspecificity of *I. dammini* and *I. scapularis* include hybridization and assortative mating experiments, morphometric comparisons, chromosome and isozyme analyses, and laboratory life cycles (Oliver et al., 1993b). Earlier data indicated similar laboratory vector competency of *B. burgdorferi* (Burgdorfer & Gage, 1986; Piesman & Sinsky, 1988) and similar host preference and feeding success in the laboratory (James & Oliver, 1990).

Additional support for conspecificity includes confirmatory chromosomal analysis (Chen et al., 1994) and comparison of sequence variation in the internal spacer regions of the ribosomal DNA genes among and within populations of *I. scapularis* and the former *I. dammini* (Wesson et al., 1993). These rDNA comparisons indicate that the geographic populations continually overlap and suggest that there is a continual gene flow (Wesson et al., 1993). Subsequent analysis of the variation in rDNA ITS1 among eastern U.S. populations of *I. scapularis* indicates only 23% sequence variation occurs between regions (Georgia, Florida vs. North Carolina, Maryland vs. Massachusetts, New Jersey, New York), but 77% variation occurs within regions. This further supports the concept that all of the *I. scapularis* populations constitute a single species (McLain et al., 1995). Moreover, lack of evidence of clear differentiation between northern and southern populations was shown in a study on the phylogeny of ticks based on mitochondrial 16S ribosomal DNA sequences (Black & Piesman, 1994). While the latter work is not focused on the question

of conspecificity or on intensive examination of genetic structure, the sequence substitution rate between the individuals sampled from North Carolina and Massachusetts is equal to that found intraspecifically in the ticks *Amblyomma americanum* (L.) and *A. variegatum* (Fabricius). A more recent investigation dealing with molecular genetic variation of the 16S and 12S mitochondrial genes of *I. scapularis* from northern and southern populations indicates much more genetic variation within southern populations (Norris et al., 1996). Almost 200 specimens of *I. scapularis* from numerous populations in the Northeast, the Southeast, and the northern and southern Midwest were examined using single strand conformation polymorphism (SSCP) according to the methods of Hiss et al. (1994). Parts of the idiosoma from each specimen were used for PCR and the remaining parts (capitulum, coxae, and legs) were examined by J. E. Keirans (Curator, U.S. National Tick Collection) to confirm morphological identifications. Twelve to fourteen different presumptive haplotypes were examined among the different regions. Genetic variants were present among ticks from different populations even within the same states (for example, Georgia, North Carolina, and Oklahoma). Although the frequencies of haplotypes differed among the regions, there were no haplotypes that were unique to any one region. Moreover, morphological types were continuously distributed among the regions.

An expanded multivariate morphometric analysis of specimens from Minnesota, Massachusetts, Maryland, Missouri, North Carolina, Georgia, F_1 progeny from reciprocal crosses between specimens from Massachusetts and Georgia, and *I. pacificus* Cooley & Kohls from California for comparison, indicates that "*I. scapularis* appears to be a polytypic species with a widespread geographic distribution in eastern North America" (Hutcheson et al., 1995). The analysis indicates latitudinal (Massachusetts–Georgia) and longitudinal (Georgia–Missouri; Minnesota–Massachusetts) clines. Measurements of 28 morphological characters of nymphs are continuous in contrast to meristic, and the pattern of geographic variation is overlapping in contrast to disjunct. Hybrids resulting from MA × GA crosses appear morphologically intermediate between northern and southern morphotypes.

Heterogeneity of *Borrelia burgdorferi*

As noted in the section on etiologic agents, *Borrelia burgdorferi* sensu lato is currently considered to be composed of four "genospecies," including *B. burgdorferi* sensu stricto, which includes the type strain B-31 (Johnson et al., 1984; Baranton et al., 1992), *B. garinii* (Baranton et al., 1992), *B. afzelii* (Canica et al., 1993), and *B. japonica* (Kawabata et al., 1993). The first three "genospecies" occur in Europe; only *B. burgdorferi* sensu stricto is thus far reported from the United States. *Borrelia garinii*, *B. afzelii*, and *B. japonica* are known from Japan; it is unknown if *B. japonica* causes disease in humans. Prior to the recognition that *B. burgdorferi* consisted of four "genospecies," several investigators noted that European isolates of *B. burgdorferi* are more heterogeneous than those from the United States (Barbour et al., 1984; Anderson et al., 1989; LeFebvre et al., 1990; Anderson, 1991; Wilske et al., 1992). Although most *B. burgdorferi* strains from the northeastern United States appear to be rather similar, exceptions do occur.

Exceptions include the antigenically variable *Borrelia burgdorferi* isolated from cottontail rabbits (*Sylvilagus floridanus*) and *Ixodes dentatus* from New York (Anderson et al., 1989); an isolate from a veery songbird (Anderson et al., 1986; Barbour et al., 1985); a strain (25015) from *I. scapularis* from Millbrook, New York (Anderson et al., 1988; Fikrig et al., 1992); and perhaps others. *Borrelia burgdorferi* strains isolated from California appear to be antigenically quite variable (Brown & Lane, 1992) and more so than strains from the northeastern United States. Strain DN127 from *I. pacificus* (Bissett & Hill, 1987; Bissett et al., 1988) and strains from *I. neotomae* (Lane & Pascocello, 1989) and *I. spinipalpis* (Craven & Dennis, 1993) are especially unusual (David Persing, pers. comm.).

Clinical symptoms of human Lyme disease patients in Europe and the United States are similar in several respects. However, as already stated, less arthritic but more neurologic symptoms are reported in European than American patients. Further, an acute dermatological condition known as acrodermatitis chronica atrophicans occurs in some European patients but is extremely rare in the United States. *Borrelia afzelii* appears to be associated with late cutaneous manifestations (Canica et al., 1993) in European patients, and as mentioned above, has not been reported from the United States. Although not thoroughly substantiated, it has been suggested that perhaps each "genospecies" might produce some common clinical symptoms in patients and yet may also be associated more often with particular symptoms not often produced by other "genospecies." For example, in a study of European Lyme disease patients, infections due to VS461 (= *B. afzelii*) were associated with cutaneous symptoms, whereas extracutaneous symptoms involved *B. garinii* (van Dam et al., 1993). More research is

needed before this observed correlation can be considered widespread.

In general, there does appear to be a great deal of consistency among the *B. burgdorferi* isolates from the northern United States and similar clinical symptoms in patients from these areas. In contrast, persons in the south that are diagnosed with Lyme disease rarely exhibit arthritis that unequivocally can be attributed to Lyme disease. The patients may present with classic erythema migrans (EM) dermatologic lesions, flu-like and/or neurologic symptoms, yet rarely with arthritis. Since it is accepted that patients in Europe have fewer occurrences of arthritic but more neurologic symptoms and acrodermatitis chronica atrophicans, it seems reasonable to suggest that perhaps patients in the southern United States might present with some but not all of the symptoms common in patients from the north. This suggestion might be more appealing if it were shown that *B. burgdorferi* is geographically widely distributed in the south, occurs commonly, and is maintained enzootically among wild animals; and if *B. burgdorferi* in the south were genetically heterogeneous, with some strains similar to those in the north and with others different. Currently, it appears that these requisites are being fulfilled.

Recently, isolates from Oklahoma (Kocan et al., 1992), Texas (Teltow et al., 1991), Missouri (Oliver et al., unpublished), Georgia (Oliver et al., 1993a), Florida (Oliver et al., 1995), North Carolina (Levine et al., 1993; Levin et al., 1995), and Virginia (Sonenshine et al., 1993) demonstrate that *Borrelia burgdorferi* is much more widely distributed than originally assumed. Most of these isolates have yet to be thoroughly analyzed; however, the few that have been characterized, especially from Missouri, Georgia, and Florida (Oliver et al., 1993a; Oliver et al., 1995; Oliver et al., unpublished), show more variability than most northern isolates thus far reported. Isolates of *B. burgdorferi* from cotton rats, cotton mice, woodrats, and the ticks *I. scapularis* and *I. dentatus* from Georgia, Florida, and Missouri show considerable heterogeneity among themselves and differences from most northeastern strains based on immunologic (monoclonal antibodies), protein (SDS-PAGE), and genetic (PCR) analyses (Oliver et al., 1993a; Oliver et al., 1995; Oliver et al., unpublished). Some strains also differ significantly in infectivity to mice (Sanders & Oliver, 1995; Oliver et al., unpublished). Pulsed-field gel electrophoresis (PFGE) analysis and DNA sequencing of a portion of the gene encoding the large ribosomal subunit 23S also support the hypothesis of greater genetic heterogeneity among spirochetes isolated from the southeastern United States than that found in isolates from the northeastern and Great Lakes regions (Persing & Oliver, unpublished data).

For example, a PFGE analysis of more than 200 *Borrelia burgdorferi* sensu lato isolates from throughout the United States, and including several from Europe, demonstrates a greater degree of genetic heterogeneity among southern isolates. *Borrelia hermsii*, a species causing relapsing fever and transmitted by the argasid tick *Ornithodoros hermsi* in the western United States, is used as an outgroup for comparison to the *B. burgdorferi* sensu lato isolates. *Borrelia hermsii* is different from all *B. burgdorferi* isolates. Among the latter, an isolate of *B. garinii* from Sweden (NBS16) and one from Russia (IP90) appear distinct from the others. The remainder form two major assemblages: one composed of type strain B31, many isolates from the northeastern and Great Lakes regions of the United States, and a few isolates from the southeastern U.S. and California. Within the B31 assemblage, three of the subdivision groups of isolates are similar to the N40 isolate from New York, whereas three other groups of isolates are more similar to the type strain B31. Five of the subdivisions contain isolates from human skin, cerebrospinal fluid, or blood. The largest number of isolates make up subdivision 5 and represent the widest geographic range as sites of origin. Sites include California, North Carolina, Florida, Wisconsin, Illinois, Massachusetts, and Connecticut. Most of the human isolates analyzed are in this group, which also includes isolates from rodents and ticks. Subdivision 6 is composed exclusively of isolates from California (human skin, woodrat, the ticks *I. pacificus* and *I. neotomae*), Georgia (cotton mouse), and two isolates from the Netherlands (human, *I. ricinus*).

The second major assemblage contains a more genetically heterogeneous group of isolates from generally more temperate climates, i.e., the southern United States and California. However, this major assemblage also contains isolates from Colorado and the 25015 strain from upstate New York. All of the isolates analyzed in this large assemblage were from non-human origin. They were isolated from rodents (cotton mice, cotton rats, woodrats, kangaroo rats) and ticks (*I. scapularis, I. dentatus, I. spinipalpis*).

Clearly, genetic analysis of *B. burgdorferi* sensu lato isolates by PFGE and DNA sequencing of a portion of the 23S gene support the contention that there is greater genetic diversity of strains in the southern and far western United States than present among strains from the northeastern and Great

Lakes regions. The trend could be even more significant than shown because relatively few southern isolates have been analyzed. It seems reasonable to consider the possibility that the heterogeneity of strains might produce variations in infectivity in humans as demonstrated in rodents (Sanders & Oliver, 1995). Perhaps different strains also produce variations in clinical symptoms and pathology as well (van Dam et al., 1993).

Distribution and Origins of *Ixodes scapularis*, *I. pacificus*, and *Borrelia burgdorferi*

The origins of *I. scapularis*, *I. pacificus*, and *B. burgdorferi* are unknown. *Ixodes scapularis* was described in 1821, but it must have been present in the United States much earlier. If it were present prior to the last Ice Age, it may well have been eliminated at that time except from the southern part of its distribution, which was not covered with glaciers. Another possible origin of *I. scapularis* might have been by the transport of *I. ricinus* from Europe to eastern North America by explorers and settlers and subsequent rapid speciation of *I. scapularis* from *I. ricinus*. As noted above, *I. scapularis* was considered a variety or subspecies of *I. ricinus* by tick experts (Nuttall & Warburton, 1911; Schulze, 1939) in the early part of the century. More recent studies (Cooley & Kohls, 1945; Keirans, 1982, 1985) list it as a separate species. We are currently investigating the species relationships among *I. scapularis*, *I. ricinus*, *I. pacificus*, and *I. persulcatus*. An hypothesis being tested is that at some point *I. scapularis* evolved from European *I. ricinus*, and *I. pacificus* evolved from Asian *I. persulcatus*. We are testing the hypothesis initially by attempting to evaluate genetic relatedness of the species. Hybridization attempts are under way between Georgia *I. scapularis* and Swiss *I. ricinus* and soon will begin between California *I. pacificus* and Russian *I. persulcatus*. The *I. scapularis* × *I. ricinus* cross has produced F_1 hybrids that have now been reared to the adult stage. Fertility of these F_1 adults is now being evaluated. Analyses of DNA sequences of various geographic populations of *I. scapularis*, *I. ricinus*, *I. pacificus*, and *I. persulcatus* are also in progress. Morphometric analyses of several southern and northern populations of *I. scapularis* indicate greater longitudinal variation among the southern (Georgia–Missouri) than among the northern (Massachusetts–Minnesota) populations (Hutcheson et al., 1995). Genetic sequence data of the mitochondrial 16S and 12S genes also indicate greater variability among southern populations (Norris et al., 1995). Shannon diversity indices of mitochondrial haplotypes calculated from haplotype frequencies among the southeastern, midwestern, and northeastern populations indicate greatest genetic diversity in the southeast, least diversity in the northeast, and intermediate diversity in the midwest (Norris et al., 1995). There was approximately three times more diversity in the southeastern than in the northeastern populations that were analyzed. Most phylogenetic analyses assume, and for some species it has been shown empirically (Baker & Stebbins, 1965), that genetic diversity is greatest in regions from which a species or population originates. The opposite view would be difficult to explain based on traditional models of migration and range expansion. This suggests that the *I. scapularis* tick populations in the northeastern areas may have been derived from those in the southeastern United States.

Using the same rationale applied above to the origin and distribution of the tick *Ixodes scapularis*, it is noted that there appears to be greater diversity of *Borrelia burgdorferi* sensu lato in Europe compared to the United States. If this concept does not change after additional isolates from southern and western U.S. locations are thoroughly analyzed, it would suggest that *B. burgdorferi* sensu lato may have been present longer in Europe. If the same rationale of greater genetic diversity is applied to origin and distribution of the spirochete in the United States, it appears that *B. burgdorferi* may have been present in the southern United States earlier than in the north. This notion is counter to the commonly held assumption that *B. burgdorferi* is currently extending its geographic range from the hyperendemic Lyme disease region of the northeast to other regions. Indeed, as already noted, until now many persons presumed, in the absence of data, that *B. burgdorferi* did not occur in the south. Data presented earlier in this paper and elsewhere disputes that presumption. Current data, much of which have yet to be published, indicate that *B. burgdorferi* is widely distributed in the southeastern states and is abundant in some locations along the south Atlantic coast.

Data on the antiquity of *Borrelia burgdorferi* in North America are limited to two reports. Persing et al. (1990) reported *B. burgdorferi* specific DNA (using polymerase chain reaction techniques) in museum tick specimens that were collected from Long Island, New York, in 1945 and in mouse specimens collected from Massachusetts in 1894 (Marshall et al., 1994). Similar analyses have yet to be reported using ticks and mammals from the southern United States. In any event, such analyses are likely to be based on relatively recent specimens

and it seems likely that the tick/*B. burgdorferi* cycle is one of great antiquity, dating back hundreds of years, perhaps to the last Ice Age.

Conclusions

The discipline of systematics is one of the foundations of science. Taxonomy of arthropod vectors and of the microorganisms harbored and transmitted by them has an enormous impact on public health globally. Taxonomic identification of arthropod vectors and pathogenic microorganisms is necessary if we are to make informed decisions about strategies to control existent and emerging diseases. Intervention in disease requires a knowledge of the identity of the causative organisms involved and their taxonomic relationships to related species. Society is best served when systematics and taxonomy utilize traditional and newer molecular techniques concurrently to focus on particular questions or problems. Science administrators, politicians, and the general public need to be informed of the importance of systematics to public health, agriculture, environmental issues, and other areas of immediate human welfare, as well as its pivotal role in inventories of biological diversity on planet Earth. Unfortunately, many taxonomic specialists are nearing retirement age and upon retirement are not being replaced. The alarming report, "Endangered Species: Doctoral Students in Systematic Entomology" (Daly, 1995), notes that such students in the United States and Canada have declined from 155 in 1982 to 111 in 1992 (28% drop) and that 40% of the departments surveyed that have insect systematists on their faculties have no doctoral students in this field.

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SYSTEMATICS AND THE CONSERVATION OF BIOLOGICAL DIVERSITY[1]

R. I. Vane-Wright[2]

Abstract

This paper concerns the role of systematics in efforts to conserve biological diversity. Biodiversity is seen both as an interdisciplinary science (involving ecology and population biology as well as systematics), and as a socio-political activity (because of the strongly anthropocentric focus of the Convention on Biological Diversity). Systematics has a number of key roles to play, especially with respect to maximizing our limited and fragmentary knowledge of biology through the predictive power of natural classification, and in helping to set priorities for conservation when, as is inevitably the case, resources are limited. After examining ways in which systematists must support the growing needs of society to know more about the Earth's biota, it is concluded that, because of their unique insights into the subject, systematists have an equally strong responsibility to take an active lead in many of the issues relating to the study, use, and conservation of biological diversity.

Dan Janzen (1993) has asked "What does tropical society want from the taxonomist?" In relation to the urgent need to know more about biological diversity, this question raises further issues—notably, is biodiversity only really important in the tropics, and does taxonomy only have a supporting role in the study of biodiversity? Here I will discuss all three questions, taking the view that taxonomists, and systematists in general, need to be proactive as well as supportive in their work.

Should Systematists Take a Lead in the Study of Biodiversity?

The subtitle of *Global Biodiversity Strategy* (Reid et al., 1992), one of the key documents produced before the 1992 UNCED conference, is "Guidelines for action to save, study, and use Earth's biotic wealth sustainably and equitably." The earlier *Caring for the Earth* (IUCN/UNEP/WWF, 1991) has the subtitle "A strategy for sustainable living." The primary objectives of the Convention on Biological Diversity are "the conservation of biological diversity . . . the sustainable use of its components . . . and the fair and equitable sharing of the benefits arising from the use of genetic resources" (Glowka et al., 1994). Thus many of these goals are unashamedly anthropocentric and primarily concerned with conservation for human benefit, rather than preservation of wildlife for its own sake.

Whether or not this "rampant, unapologetic utilitarianism" (Porritt, 1994) is the best strategy is open to debate (e.g., Allen & Edwards, 1995; Oates, 1995), but this is where most of the force behind national and international conservation efforts is now located. The Global Environment Facility (Glowka et al., 1994), the interim financial mechanism of the Convention (currently administered by the World Bank), is the largest single source of funding ever made available for work on biodiversity—a funding source which systematists seem surprisingly slow to exploit. As Robert May (1990) has observed, "Without taxonomy to give shape to the bricks, and systematics to tell us how to put them together, the house of biological science is a meaningless jumble." If systematics provides the foundation of our understanding and ability to communicate about biological diversity, what role should systematists seek to play in the study, use, and conservation of the Earth's biotic wealth?

What is Biodiversity?

An impression can readily be formed from much of the modern bioscience literature that the study of biological diversity is the preserve, not of systematics, but of ecology. The study of diversity rests neither with one nor the other, but with both. Biodiversity exists at the interface of pattern and process, as for example in the twin hierarchy envisaged by Eldredge and Salthe (1984; Table 1), in phylogenetics and population genetics (the distinc-

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Table 1. The twin biological hierarchy (based on Eldredge & Salthe, 1984).

Genealogical hierarchy [pattern]	Ecological hierarchy [process]
Codons	Enzymes
Genes	Cells
Organisms [individuation]	Organisms [physiological function]
Demes	Populations
Species	Local ecosystems
Monophyletic taxa	Biotic regions
All life	Entire biosphere

tion between phylogenetic and tokogenetic relationships: Hennig, 1966), and in historical versus ecological biogeography (Myers & Giller, 1988).

Olivier Rieppel (1988) has discussed in depth a number of the scientific and philosophical issues of the pattern versus process debate. He observed that the analysis of pattern and process represents different and incompatible "ways of seeing," as "the first emphasises discontinuity, while the other is based on the principle of continuity." The two are complementary because pattern analysis offers the only guide to common ancestry, and so gives direction to the analysis of process, while process analysis is the only way of giving pattern a causal explanation. He finally concluded, given we have different ways of seeing biology, that we should accept that each has its merits and faults, and that each is incomplete by itself. Being complementary, we should make use of both approaches to get as complete a picture of biology as possible (Rieppel, 1988, esp. 170–171). Because of this intimate interrelationship, it is essential that systematists work together with ecologists and population biologists to develop a fuller understanding of biological diversity, including its potential uses—and, most urgently, to develop more effective strategies for its conservation.

SYSTEMATICS AND THE USE OF BIODIVERSITY

Current estimates of the number of extant species of organisms vary from 3 to 100 million; Hammond (1992) gave a carefully considered estimate of 12.5 million, but confidence limits on such figures are incalculable. There is greater agreement about the number of species that have been formally described (in the region of 1.5–1.8 million) but, even so, the uncertainties of synonymy ensure that the limits remain difficult to assess (Solow et al., 1995). The complications of heterozygosity, variation in genome size and degree of similarity/dissimilarity between species, and basic uncertainties about how to delimit the number of genes even in well-known organisms, compound any attempt to estimate the protean diversity that occurs at the genetic level. Undeterred, Wilson (1992) has estimated something in the order of 10^{17} nucleotide pairs as specifying the diversity among species, together with more than 10^{18} gene combinations potentially available per typical species. Taxonomists might seem like chemists with a knowledge of 10 elements from the Periodic Table, while geneticists might be compared to physicists trying to understand the Universe from the behavior of just a single fundamental particle. Is our ignorance of the biosphere really so extreme?

In 1973 a mealybug was discovered attacking cassava in Africa. By the end of 1989 this pest was causing massive crop losses throughout the African tropics. Initial attempts to find a natural biocontrol agent failed, until it was realized that the mealybug was part of an undescribed species complex, and that it only occurred naturally in the southern Neotropics (Cox & Williams, 1981). An appropriate encyrtid wasp was then found, tested, and introduced into Africa. The wasp has now spread over more than 12 million km^2 and gives effective control of the mealybug throughout its African range, with an annual cost benefit estimated at $200,000,000 (Herren & Neuenschwander, 1991).

This example, involving a new pest and an equally unknown biocontrol agent, tells us something special about the nature of our ignorance. Biology has to deal with a staggering number of specifics—there are thousands of mealybugs, and tens of thousands of encyrtid wasps. To solve the problem, entomologists had to find out precisely *which* mealybug they were dealing with, locate this species in its natural habitat, and discover precisely which of all those wasps was *one that attacked it.* The only reason this could be done quickly is because the existing classification of bugs and wasps, however incomplete, is sufficient to form a valid basis for *prediction.* Once the mealybug had been accurately located in the system, it was possible to predict its geographical origin, and then what sort of insect to look out for as a natural biocontrol agent. Our detailed knowledge of the biology of all these myriad species inevitably lags behind our knowledge of their classification, but the natural system allows us to extrapolate what knowledge we do have.

Thus our ignorance of biology, while profound, is manageable insofar as our classifications are predictive. Far from being a passive pigeon-holing activity as some seem to believe, classification has all

the properties of an intelligence system, often allowing us to go far beyond the seemingly limited information available. Although there are literally millions of undescribed species, nearly all animals and plants can readily be placed within meaningful families. Like hypotheses, good classifications "allow limited data to be used with remarkable effect, by allowing interpolations through data-gaps, and extrapolations to be made to new situations for which data are not available" (Gregory, 1980).

One of the most frequently proposed uses for biodiversity is biochemical prospecting. Costa Rica's INBio has even formed contractual agreements with international pharmaceutical companies. Gámez and Gauld (1993), in describing the Costa Rican experience, suggested that the Hymenoptera, with their multitude of species and pharmacologically active venoms and other secretions, are a potentially excellent source of valuable new chemicals. While this is undoubtedly true, the same can be said for almost any diverse group.

Schulz et al. (1993) examined the male pheromone-gland secretions of 10 African milkweed butterflies, separating 214 substances in 14 chemical classes. Individual species had from 12 to 59 compounds (excluding tetrahydrofurans, which were not systematically investigated), including a high proportion restricted to individual species, or just a few, usually closely related species. Among these were some compounds rarely or never found in nature before, such as the ketone 16-heptadecen-2-one from *Amauris hecate*, and the monoterpene (*E*)-2,6-dimethyl-5-octen-1,8-diol from *Danaus chrysippus*. If we wished to prospect for closely related substances in other species, the existing cladistic classification (Ackery & Vane-Wright, 1984) would give us immediate and obvious clues—such as the chemically uninvestigated *Amauris dannfelti* and *A. inferna* for the ketone, and *Danaus gilippus* for the terpene.

This suggests that, armed with an appropriate classification, chemical prospecting need not be "blind": if we find something interesting, we can look at closely related species with the heightened expectation of finding more of the same or related compounds. If, on the other hand, we want to select, say, the 10 most different species out of a sample of 1000, to maximize the chance of finding radically different chemicals per unit effort, we can make use of the diversity measurements developed in systematic conservation evaluation (see below). Either way, the natural classification offers the most intelligent basis for biochemical prospecting, or for any other use that depends on predicting the biological properties of organisms. The better our classifications are, the more explanatory power they will have (Farris, 1979, 1983), and the more effective they will be for making such predictions.

SYSTEMATICS AND CONSERVING BIODIVERSITY

There are two major strands to conservation biology: where to conserve living things, and how to conserve them (Caughley, 1994). The latter represents a major application of ecology and population biology. Regarding the former, systematists have been closely involved with recent developments (e.g., see Forey et al., 1994), including the formulation of new approaches to measuring diversity that take account of phylogenetic relationships.

According to Taylor (1978), the notion of diversity, as an interrelation of species richness and individual abundance, was first recognized by Henry Walter Bates. Bates's idea, to evaluate the diversity of a locality and compare it with that of another, was later formalized as α-diversity (Whittaker, 1965). Whittaker (1972), while elaborating a more complex scheme (α-, β- and δ-diversity) to take account of species turnover at varying spatial scales (Magurran, 1988, gave a review of the considerable variety of procedures that have now been proposed for the measurement of "ecological diversity"), also suggested that time, in addition to richness and spatial turnover, should be included in a more complete expression of diversity. Time is the primary dimension of evolution along which differences between lineages accumulate.

Conservation biologists, concerned with the need to set priorities for the preservation of genetic diversity, have recognized the same problem and proposed that this could be solved, to a first approximation, by mobilizing information contained within the taxonomic hierarchy: "The size of the potential genetic loss is related to the taxonomic hierarchy because, ideally at least, different positions in this hierarchy reflect greater or lesser degrees of genetic difference and hence differences in such variables as morphology, behaviour, physiology, chemistry and ecology. Although the degree of difference (the gap) between genera and between species within genera varies both within and among classes, the current taxonomic hierarchy provides the only convenient rule of thumb for determining the relative size of a potential loss of genetic material" (IUCN/ UNEP/ WWF, 1980).

Vane-Wright et al. (1991) proposed a diversity metric sensitive both to individual taxonomic (hierarchical, not formal) rank and total number of species found within an area. This index, subsequently called root-weight, was the first formal measurement of taxic diversity. In a series of pa-

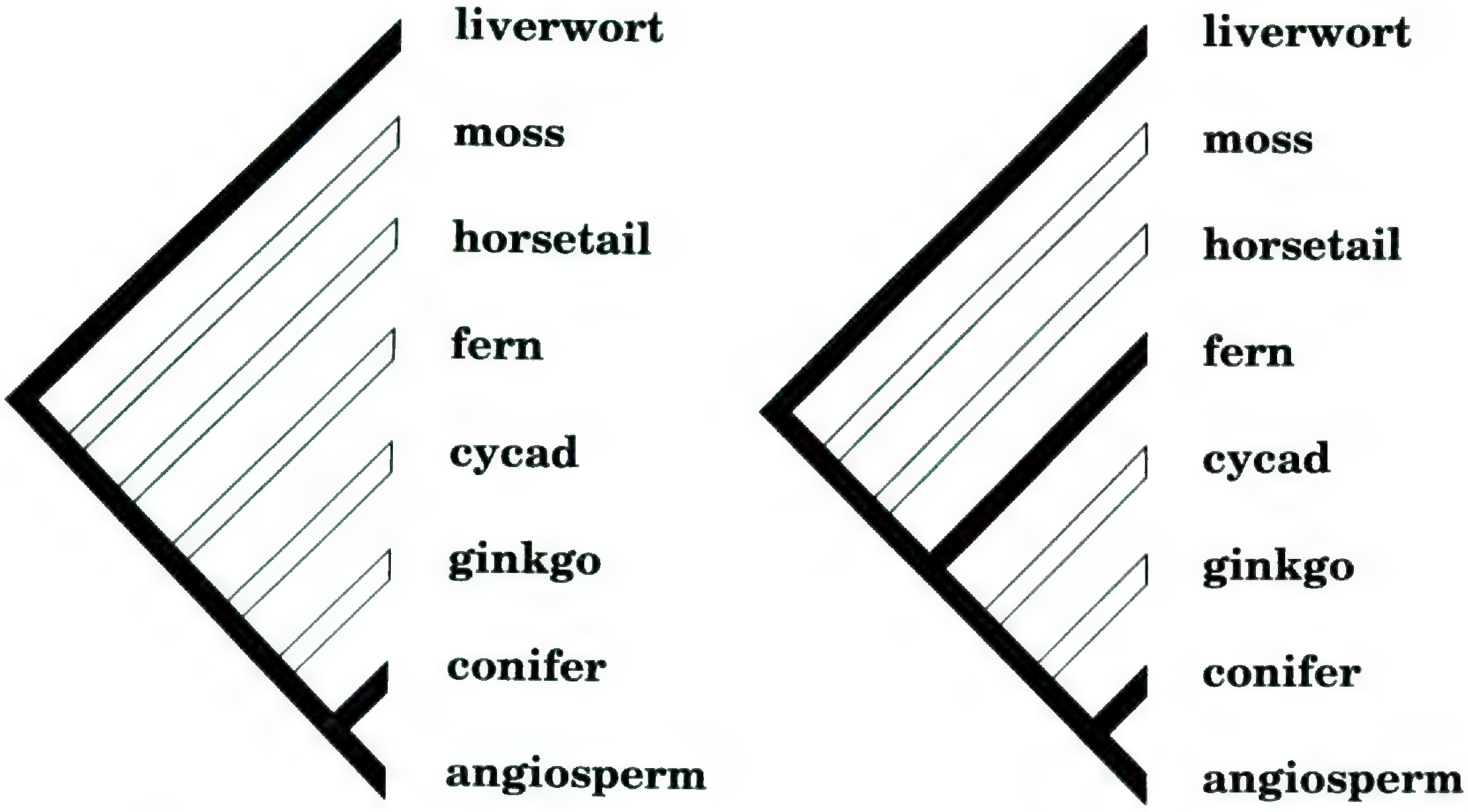

Figure 1. Choosing three land plants from eight: based on the cladogram, which combination would maximize biodiversity? Character richness (on the left) chooses liverwort, conifer or angiosperm, plus any one of the series moss–*Ginkgo*; character combination richness (right) selects liverwort, fern, and conifer or angiosperm. (Assuming all character changes are associated only with nodes shown and a comparable number of character changes occur at each node; based on Williams & Humphries, 1994; hierarchical relationships of plants from Humphries & Parenti, 1986.) See text for explanation.

pers, notably those of Williams (e.g., Williams, 1993; Williams et al., 1991, 1993, 1995; Humphries & Williams, 1994), Weitzman (1992), Nixon and Wheeler (1992), and Faith (e.g., 1992, 1994), the concept of taxic diversity has been refined and clarified—notably with respect to the fundamental question of what is being measured, and why.

Humphries et al. (1995) concluded that the current goal is to assess option value. This concept offers "a means of assigning a value to risk aversion in the face of uncertainty" (McNeely, 1988), and can be related to the task of "maximising the human capacity to adapt to changing ecological conditions" (Reid, 1994). If this is accepted, then we can abandon the insoluble problem of trying to assign fixed values to individual species (Ehrenfeld, 1988) and focus our attention instead at the level of expressible and heritable characters (genes, traits, features, etc.; Faith, 1992, 1994; Williams et al., 1995), which, collectively, can be considered to represent the fundamental currency units of option value.

Thus a set of species can be evaluated in terms of the total number of different characters they represent. The impact of losing (or the addition of) any particular species can be measured in the same way, thus fulfilling the need to assess "the size of potential genetic loss" (or gain). In practice, however, it is impossible to measure character differences directly on a large enough scale, and so the distribution of characters across taxa has to be modeled. It is now agreed that this should be based on the genealogical hierarchy, as expressed more and more accurately by taxonomic ranks, cladograms, and phylogenetic trees. Debate continues, however, regarding which model of character change should be applied (e.g., empirical versus anagenetic versus cladogenetic), and whether or not differences should then be assessed in terms of character richness only, or character combination richness (Williams et al., 1995).

Some idea of the two approaches is given by Figure 1. Suppose we could only select for conservation three of the eight land plant species shown. If species richness were the only criterion, then any of the 56 combinations of 3 species from 8 would be equally acceptable. But if we interpret the tree subtending the eight species as a statement about their mutual phylogenetic relationships, then on the basis of just this information (making the assumption that a comparable number of character changes occur between each node shown), only 10 combinations will maximize character richness (liverwort plus conifer or angiosperm, plus any one from the

Table 2. Complementarity: the eight plants listed in Figure 1 have been allocated to five hypothetical areas; l = liverwort, m = moss, f = fern, y = cycad, g = ginkgo, n = conifer, a = angiosperm, h = horsetail. (Based on Underhill, 1994; see text for explanation.)

Species:	l	m	f	y	g	n	a	h
Area 1	−	−	+	+	+	+	+	−
2	+	+	+	+	−	−	−	−
3	−	−	−	−	+	+	+	+
4	+	+	+	−	−	−	−	−
5	−	−	−	−	−	+	+	+

series moss-*Ginkgo*). Alternatively, we could choose to maximize character combination richness, but then only two possible combinations are selected: liverwort, fern, plus conifer or angiosperm. (The root-weight index, if the cladogram is rooted between liverwort and moss, would restrict the choice to liverwort, moss, and horsetail—but this index is no longer regarded as appropriate.) Despite some significant differences in these results, when large numbers of taxa are involved, simple species richness for an area usually turns out to be a good approximation for both character richness and character combination richness (Williams & Humphries, 1994).

We now seem close to a satisfactory theoretical basis for at least part of what May (1990) has called the "calculus of biodiversity." Another, and perhaps even more significant aspect of the procedure, is provided by the concept of complementarity.

Where Is Biodiversity Most Important?

COMPLEMENTARITY AND ITS IMPLICATIONS

In Table 2 the eight land plants in Figure 1 have been allocated to five areas. Suppose you were told that you could only choose one area for conservation, which would you select? Guided by species richness alone, area 1 would seem an obvious choice. What if you were then asked to add a second area? The greatest number of additional species to the five already represented by area 1 is two (liverwort and moss), both of which can be added by area 2 or area 4. Area 1 plus area 2 or 4 can thus account for seven of the eight species; the eighth (horsetail) could then be added by a third area (3 or 5). If, however, you were asked to select just sufficient areas from the outset to represent all eight species, it is obvious by inspection of Table 2 that areas 2 and 3 together include all of them, giving a more efficient final solution than adding areas step by step, starting with the richest first.

In reality both procedures have a place. Often it may not be possible to represent all species, vegetation types, or land forms from the outset, in which case a step-wise procedure may be the most appropriate. In other cases, it may be possible to select from the beginning a set of areas to represent all known (or vulnerable, etc.) biological attributes in a region, in which case a set-wise procedure will usually offer a more efficient analysis. (In this particular example, it is interesting to note that application of a taxic diversity index, such as character richness, identifies both areas 2 and 3 as richer than area 1, based on the hierarchy given in Figure 1, illustrating the point that species richness should not be regarded as the sole determinant of taxic diversity.)

Both the step-wise and set-wise procedures reflect the idea of complementarity: the degree to which specified areas, singly or in combination, represent the species or taxic diversity of an entire group or set of groups. Complementarity, first applied by Kirkpatrick (1983) and Ackery and Vane-Wright (1984), and formalized by Vane-Wright et al. (1991; see also Margules et al., 1988; Rebelo & Siegfried, 1992; Pressey et al., 1993; Faith, 1994; Williams & Humphries, 1994) has much in common with β- and δ-diversity but, crucially, instead of just reducing taxon turnover to numerical values or indices, information on the identity of taxa between areas is retained.

Although deceptively simple, the emergence of the idea of complementarity has been significant for biodiversity evaluation. This is because it has shifted attention from assessing areas on an absolute scale (e.g., richness or scoring index) to a relational scale (taking account of spatial turnover). In this way, all areas can be seen as part of a whole. For example, while tropical forests and coral reefs may be the richest biological systems on Earth, the very distinct biota of other ecosystems, such as those of ocean bottoms or the relatively species-poor higher latitudes, also have a unique contribution to make (Table 3). Complementarity provides a basic criterion for efficient and goal-directed procedures of area selection.

PRIORITIES IN CONTEXT

If we take into account quantitative effects of biodiversity (Cousins, 1994), particularly in relation, for example, to ecosystem services (Ehrlich & Daily, 1993), or the value of local biodiversity to humanity (Gadgil, 1991, 1992), it is evident that all areas of the Earth should be seen as important. Recognizing unique value for a particular area does

Table 3. Essentially extratropical plant familes (from Heywood et al., 1978). Most contain only one or a few species.

S. Hemisphere	N. Hemisphere	Bipolar
Lactoridaceae	Trochodendraceae	Lardizabalaceae
Gomortegaceae	Cercidiphyllaceae	Empetraceae
Malesherbiaceae	Eucommiaceae	Juncaginaceae
Achariaceae	Leitneriaceae	Posidoniaceae
Grubbiaceae	Paeoniaceae	
Cephalotaceae	Diapensiaceae	
Penaeaceae	Theligonaceae	
Misodendraceae	Hippuridaceae	
Geissolomataceae	Cynomoriaceae	
Calyceraceae	Cneoraceae	
	Limnanthaceae	
	Phrymaceae	
	Adoxaceae	
	Butomaceae	
	Scheuchzeriaceae	

not mean that adjacent areas are unimportant, or that they can be abused with impunity. Priorities should not be seen as merely choosing a few of the richest, or even most complementary sites, but more in differential allocation of resources (Vane-Wright, in press) to do the best we can, in relation to relative importance both in terms of pattern and process, across all areas of land and sea. Nevertheless, for the establishment of a network of special areas to act as reserves to ensure that as much of the irreplaceable qualitatively different (genealogical) elements of diversity survive, and are thus available to future generations, analyses based on complementarity among areas supporting vulnerable attributes (gene, species, assemblages) will be of great importance if the limited resources currently available for biodiversity conservation are to be used to maximum effect (Pressey et al., 1993; Pressey, 1994). The whole must be managed as effectively and sensitively as possible; within such a whole, a network of special reserve or management sites for biodiversity then has special significance and can serve a useful function.

What Should Systematists Do For Society?

REACTION

Commenting on his own question, "What does tropical society want from the taxonomist?", Dan Janzen (1993) observed that "The wording of the chapter heading is the message. I do not ask 'What does the taxonomist have to offer tropical society?' Tropical society's needs recently have been, can be and should be a major rejuvenating force in systematics." According to this view society and, in particular, tropical society, is looking to systematists to make certain things possible. First and foremost, according to Janzen, a "cleaned up" set of names and a manageable system is needed for "filing, comparing, searching, recording and working with the species . . . that constitute the . . . bountiful biodiversity resource of tropical nations." Based on Janzen's ideas, and those of others like Stork (1994) and Nielsen and West (1994), I list below some areas in which systematists are being called upon to respond.

General attitude change. There is a need to demystify taxonomy and, in the process, make taxonomic products (such as identification systems and catalogues) more accessible (Miller, 1994). Much of this attitude change relates to gathering systematic data in the first place, and processing it in a way that not only offers self-satisfaction (peer group approval), but also satisfies the rapidly expanding needs of non-specialists.

Improved taxon sampling, recording, and storage. Better distributional data, including bionomic information such as host associations, etc., are essential (Wheeler, 1995; McNeely, 1995). Existing information is often based on ad hoc sampling procedures, resulting in a partial and disconnected coverage. Systematists should become involved with radical approaches to rational and cost-effective methods for data collection and spatial modeling, as well as application of techniques for improving estimates of distributional patterns based on existing data (Margules & Austin, 1991, 1994). This need includes dealing with the almost overwhelming number of (mainly species-level) taxa that remain unrecognized and undifferentiated (Wilson, 1992). Once biological samples have been

made, their continuing availability in well-documented and properly curated collections is fundamental to future work, including the extraction of information (such as DNA data) not necessarily considered at the time of original acquisition (Vane-Wright & Cranston, 1992).

Better systematic analysis. Because knowledge of the Earth's biota will inevitably remain incomplete, I have argued above that it is essential to place what knowledge we do have in as powerful a predictive system as possible (cf. Nielsen & West, 1994). This applies not only to the primary activity of classification, where phylogenetic methodology should be pursued vigorously in building a natural system, but also to secondary disciplines such as biogeography where, for example, the possibility of recognizing areas of endemism still offers much in terms of predictive power, or information (Platnick, 1991).

User-oriented databases. In order to make systematic, taxonomic, distributional, and bionomic data, together with information about the uses and values of different organisms, as widely available as possible, user-oriented electronic databases must be developed and made widely available by appropriate means (e.g., Internet: Miller, 1994; cf. Cracraft, 1995). In order to do this, it has to be understood that continuing problems will occur over costs and intellectual property rights, and these problems (including cost recovery and academic recognition) need to be solved.

Improved use of advanced technology. As part of the inevitable change to electronic methods for storing, analyzing and making systematic data more widely available, every opportunity should be taken to make increasingly imaginative use of computer and video technology. One of the most obvious areas lies in the development of fully illustrated, multiple-entry, interactive keys (currently based, for example, on CD-ROM technology: e.g., ETI, 1992; Watson & Dallwitz, 1993), but many other opportunities exist, such as the production of special checklists or other products tailored to fulfill unique needs, or the application of shape-analysis to identification. Other advances in biotechnology, leading to automated identification procedures based on blood or other tissue samples, or rapid increases in the quantity and quality of sequence data, must also be expected. The community of systematists should embrace these positive and exciting developments because, so long as they are properly set up, such information systems will give systematists more time to develop their basic and traditional taxonomic skills—skills that will remain fundamental to further development and application of systematics to the problems of biodiversity.

Training new systematists. Under this heading we must acknowledge the need not only to be involved in training new generations of systematists, but also with institution building, such as the creation of new museums and reference collections. Assistance with the development of national biodiversity institutes (Gámez & Gauld, 1993) is likely to represent a particular challenge.

Involvement with biodiversity projects. The emergence of "biodiversity" as a topic (Harper & Hawksworth, 1994) raises many issues, not least of which is the fear that it may only represent a transient "band-wagon," likely to run out of steam or backfire on those who become too deeply committed. On the contrary, because the concept links concerns over the preservation of nature and its use directly to the needs of human society, it represents a fundamentally new way of thinking about biological diversity. Systematists need to play their part in the support of biodiversity projects, including such diverse activities as preparing user-friendly identification systems, training parataxonomists, being involved with surveys and inventory schemes, setting up museums, reference collections, and other information systems, making conservation and environmental evaluations, and so on. Biodiversity is a key social issue (Machlis, 1992), and it is vital that systematists play their part, not least by being sensitive to and catering for user needs (including local names, natural products information, etc.—things sometimes considered outside our remit).

Involvement with education. Because biodiversity is important and will remain so in the future, systematists should expect to play a full and active role in building public awareness (Cracraft, 1995), including, in particular, the education of young people (e.g., Yen, 1994).

PROACTION

The activities listed above are described in terms of responding to the needs of society for better, more comprehensive, and above all more accessible information about the Earth's biota and its significance. Appropriate reactions by systematists to the needs of society undoubtedly form part of our responsibilities (especially as society at large has already paid for so much of the collections, libraries, and other paraphernalia essential for our operations). However, as I will argue in the last section, it is also our responsibility to be proactive—to put

forward new ideas and create better attitudes to biodiversity by taking initiatives based on our own unique insights.

Take just one example. If we attempt to set conservation priorities based on separate analyses of the distributions of species belonging to more than one taxonomic group, it is apparent that this typically leads to different, sometimes totally different, conclusions about what actions are needed (e.g., Prendergast et al., 1993). Can such conflicts be resolved? Systematists have proposed two approaches to solving this problem: taxon summation (Vane-Wright et al., 1994), and the use of higher taxa (Williams et al., 1994). Although further work on both methods (which are not necessarily exclusive) is needed, the point here is that systematists tend to propose very different sorts of solutions than ecologists or population biologists.

Many ideas will need thorough evaluation before we settle on the most appropriate information and methods for priority areas analysis. Only by mobilizing systematic data, and creating the means to interpret it in a logical and systematic way, will we be able to develop efficient plans and monitoring schemes for conserving biodiversity. A primary goal is simply to make the most of limited resources that, inevitably, will never be enough to do everything that might be considered desirable. Systematics Agenda 2000 can lead here by promoting a network of systematists to create the wide range of species-level and higher-category databases which, together with appropriate analytical procedures, will be needed for a comprehensive approach to conservation evaluation.

OUR RESPONSIBILITIES AS SYSTEMATISTS

The burgeoning human population, driven by consumerism and poverty, is having a massively deleterious effect on biological diversity, through industrial pollution, resource appropriation, overcropping, and ecosystem transformation. We see local and global extinctions on the one hand, and the spread of a limited range of synanthropic species on the other, leading to extinction of taxa and even entire ecosystems, extirpation of myriad populations, and widespread loss of complementarity. Diversity is being diminished and homogenized.

As human demand for resources in both the developed and developing world continues to grow, so the rate of human-induced biodiversity loss accelerates. The end-point is unknown, as are the consequences. All we can say is that the biosphere, on which our life is totally dependent, will be called upon to provide more and more food, timber, and fiber, more clean water, more clean air, while absorbing more pollutants, all from a continually diminishing biotic base, quantitatively and qualitatively.

Faced with this alarming prospect, most nations have now agreed, at least in principle, to try to take some form of corrective action, to which almost universal support (at least on paper) for the Convention on Biological Diversity bears witness. This requires that each nation ratifying the Convention should pursue, through various provisions outlined, the conservation of biodiversity, the sustainable use of its components, and the fair and equitable sharing of benefits arising from the utilization of genetic resources.

As I have already suggested, this approach to biological diversity is radically different from previous concerns of the conservation movement, such as the protection of rare and endangered species, or the preservation of wilderness areas. The difference relates to the anthropocentric focus: human needs constitute both the threat and the solution. That is not to say that conservation will be compromised: on the contrary, conservation has shifted, in theory, from pressure-group status to being part of the fabric of human society. Conservation, and specifically the needs and uses of biodiversity, are now in the realm of what might be termed social engineering.

So biological diversity is, all of a sudden, big business. In relation to biological science in general, and to the community of professional conservationists, ecologists, systematists, and so on, this is good news. However, the arrival of biodiversity as a political issue does not just signal new sources of funds. We need to appreciate fully (unless we allow ourselves to be prey to the worst sort of cynicism), first that biodiversity is couched within a truly social framework (we are thus operating beyond the strict confines of science, in the areas of policy and socio-economics), and second, that we have new and expanded responsibilities that we, the community of systematists, must face up to. This includes the fact that much of the best data about biodiversity lies buried in our collections and libraries.

In my view, it is very much part of our responsibilities to take control and help shape policy through our own initiatives. We hold the best insight into the strengths and weaknesses of taxonomy and systematics. We, very largely, are paid out of public funds, and thus hold the responsibility not only to react supportively to the needs of society at large, but also to mobilize, make use of, communicate, and even lobby for the unique insights

that only we are in a position to formulate or bring to bear. Our responsibilities go beyond simply giving support when asked: we must also ensure that our knowledge and understanding are brought to the fore, to be judged useful—or not—as others decide.

Death and the Compass is the title of a short story by Jorge Luis Borges (1970). A criminal investigator has been set the task of trying to discover the murderer of a Jewish academic. At the scene of the crime, and in response to a suggestion that the scholar was accidentally murdered by somebody really intending to rob the man living next door, the investigator replies, "Possible but not interesting. You'll reply that reality hasn't the least obligation to be interesting. And I'll answer you that reality may avoid that obligation but that hypotheses may not. In the hypothesis that you propose, chance intervenes copiously. Here we have a dead rabbi; I would prefer a purely rabbinical explanation, not the imaginary mischances of an imaginary robber."

A multitude of taxa are under threat of death. In sympathy with Borges's investigator, we should not avoid the burden of providing an intellectually sound and satisfying solution. We need a systematic as well as an ecological chart of the biosphere (Eldredge & Salthe, 1984; Rieppel, 1988), and should develop a systematic plan to outwit as many imminent taxic deaths as possible. In short, we must endeavor to find what we believe to be an appropriate scientific solution, which takes full account of the principles and insights of systematics, in the same way that Borges's investigator sought an interesting explanation for the rabbi's fate.

But Borges's story carries not only this message for us, but also a dire warning. The investigator, besotted with pursuit of an intellectual game of death, ends up as the final, ultimate victim. While our work must be interesting, systematic, academically sound, it must also be timely, realistic, practical. We must be vigilant to ensure that Systematics Agenda 2000, or whatever we like to call our current game plan, is not merely self-seeking, not merely more of the same, time-worn, mutton dressed as lamb, old wine in new bottles, but really is oriented outward, toward society at large, to fulfill our responsibilities as true guardians of biological diversity.

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TRANSFORMING ETHNOBOTANY FOR THE NEW MILLENNIUM[1]

Michael J. Balick[2]

Abstract

In the past several decades, the science of ethnobotany has evolved from a discipline primarily concerned with making lists of useful plants in a particular geographic region or among an individual tribe, to a multidisciplinary endeavor focused on understanding the relationship between plants and people. Ethnobotanists are involved in projects ranging from community level germplasm conservation to multinational biodiversity prospecting. One result of the renewed interest and activity in ethnobotany has been the increased public awareness of this branch of biological science. Several projects utilizing the contemporary ethnobotanical paradigm are discussed, including *in-situ* germplasm conservation in the western United States, ethnobotanical market surveys in Mexico, the management and use of *Sabal* palm resources in Mexico, quantitative studies in the Neotropics, and ethnopharmacological studies linked to drug development in Samoa. The Belize Ethnobotany Project's multidisciplinary approach to the study and conservation of traditional medicines and the development of an ethno-biomedical forest reserve in Belize are also reviewed. Contemporary ethnobotanical studies have value not only for the research questions they address, but as a way of catalyzing awareness of the value of biological diversity and support for its conservation among a broad range of people.

The term ethnobotany was first proposed in a lecture by John Harshberger to apply to the study of "plants used by primitive and aboriginal people . . ." (Anonymous, 1895). This initial concept of ethnobotanical investigation was typified in a paper by J. Walter Fewkes (1896), "A Contribution to Ethnobotany," in which he wrote of the work of his student J. G. Owens, who initiated a study on the foods and food resources of the Hopi Indians. In this paper, which was published after Owens's death, Fewkes wrote about their collaborative endeavors, presenting a list of the common names and uses of several dozen food species, and stating, "I simply wish to call attention to the interesting field of ethnobotany which the Hopi Indians furnish the ethnologist." This work reflects the style in which early ethnobotanical studies were undertaken—compiling lists of common and Latin names of plants used by an indigenous group.

Efforts previous to that time were carried out under the heading of "aboriginal botany," a term coined by Steven Powers (1873–1875) to include "all forms of the vegetable world which the aborigines used for medicine, food, textile fabrics, ornaments, etc." Edward L. Palmer, a botanist who made comprehensive descriptions of the flora of the western United States, was also one of the first botanists to investigate the cultural significance of plants to indigenous people through his fieldwork (Palmer, 1871, 1878). Prior to the above-mentioned endeavors, other investigators studied the use of plants by North American indigenous peoples, often focusing on the medicinal values that these conferred. Ford (1978) calculated that a total of 904 studies had been published on native North American ethnobotany before 1977.

In the past several decades, the nature of ethnobotanical investigation began to change, becoming more focused on studies of the relationship between plants and people in the broadest sense, and employing multidisciplinary perspectives. Examples include the study of Berlin et al. (1974), which combined botanical, linguistic, and utilization information, and that of Schultes and Hoffman (1973), which united ethnomedicine and phytochemistry. The emergence of ethnobotany as a multidisciplinary science, springing forth from its foundation in systematic botany, has resulted in interesting and important research questions that are being addressed. This "new" ethnobotany links diverse disciplines, such as anthropology, botany, nutrition, ecology, conservation, economics, and

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pharmacology, in a way that generates new ways of thinking and a new style of scholarship. Workers in this field also recognize the need to take a much more active role in addressing important issues of human society such as biodiversity conservation, food shortage, and the development of new medicines. Contemporary ethnobotanists are also raising concerns about the ethical implications of their research endeavors—for example, who should share in the benefits of new discoveries such as medicines or foods from plants (Boom, 1990; Cunningham, 1993; Axt et al., 1993). They are also forging closer ties with government and private sector research groups working to develop new food, drug, and energy resources. One important aspect of this renaissance in the field of ethnobotany has been the increased level of public interest in this subject. Through television documentaries, movies, magazine articles, and radio interviews, the research of ethnobotanists is being used to illustrate the importance of biodiversity and its conservation. In promoting the objectives proposed by Systematics Agenda 2000, it seems obvious that current research topics in ethnobotany can attract the attention of important constituencies whose thinking we wish to influence.

This paper will highlight examples of the research activities undertaken by contemporary ethnobotanists. It will summarize several papers presented at a recent meeting of the Society for Economic Botany that provide examples of active field- and laboratory-oriented ethnobotany projects, as well as the author's efforts in Belize.

Germplasm Conservation

Recently, concern has been expressed that *ex situ* germplasm conservation may not be sufficient for preserving the genetic integrity of selected crop species or the plethora of landraces cultivated by traditional peoples. Crop plant relatives found in the wild are also at risk. Iltis (1974) suggested that *in situ* conservation was an important adjunct for *ex situ* conservation of crop plants. A combination of both strategies is now seen as desirable, in order to ensure preservation of the maximum amount of genetic diversity. *Ex situ* conservation activities have gone far beyond the intention of serving only crop breeders; such materials are seen as valuable for supporting low-input traditional agricultural systems and insuring their capacity to recover from natural disasters, as well as restoring the genetic diversity of crop varieties in traditional systems in areas where this diversity has been lost due to changes in the socioeconomic and/or biophysical environment.

Soleri and Smith (1995) investigated the results of conserving two Hopi folk varieties of *Zea mays* L. in a USDA germplasm program (*ex situ*) and by traditional farmers (*in situ*). They tested three hypotheses: "1) *Ex situ* conservation of populations of a maize folk variety results in significant changes to those populations; 2) There are no significant differences between populations of a maize folk variety maintained by Hopi farmers today; and 3) There are significant differences between a folk variety maintained *in situ* by farming households today and the same folk variety maintained *ex situ* by an institutional conservation program." Working with two traditional corn varieties, they measured significant changes in morphological characters such as anther color, glume color, glume bar, plant height, and central spike length. They concluded that, in terms of meeting the needs of traditional agriculture, the greatest concern for traditional varieties conserved using *ex situ* technology "may be the changes during conservation resulting from genetic shift as compared with genetic drift." The data collected to test the second hypothesis seemed to indicate that there were no differences between populations of a *Zea mays* folk variety maintained by contemporary Hopi farmers. Based on their data, however, they neither accepted nor rejected the hypothesis and, instead, concluded that further research would be required. The third hypothesis, suggesting significant differences between the same folk variety conserved in two different ways, was accepted. Despite the technical difficulties in testing these hypotheses it was clear that the invariable maintenance of material utilizing *ex situ* conservation methods is nearly impossible and that the two conservation strategies yield different results, demanding a reconsideration of crop genetic resources, conservation goals, and assumptions. Work such as that being done by Soleri and Smith, incorporating the ethnobotanical perspective into germplasm conservation, is clearly in the forefront of efforts to preserve crop germplasm and will, I am certain, help reshape a great deal of the future thinking on this topic.

Market Studies

Linares and Bye (1987) and their colleagues at the Jardín Botánico, Universidad Nacional Autónoma de México, have carried out exhaustive surveys of market plants in Mexico since the 1980s. Their studies, mostly focusing on medicinal and edible plants, have involved work with traditional

healers, medical doctors, herb vendors, farmers, botanists, educators, and local health promoters. Linares and Bye (1987) compared medicinal herbs sold in the markets of central and northern Mexico to those sold in the southwestern United States and found that local people group plants into folk "complexes" of species that share common names, morphological and aromatic characteristics, as well as uses. For example, the complex known in this geographic region as "*hierba antś*" comprised several genera (*Tagetes* L., *Artemisia* L., *Pimpinella* L., and *Illicium* L.), all with the characteristic odor of anise. One observation from this study is that each of the four complexes of plants investigated was "labeled" by choosing an individual plant species considered the most valuable within the complex. Each particular "label" plant tended to be sold far outside of its natural range, and local plants were often substituted during times it was unavailable. The labeled plant for the "*hierba antś*" complex was *Tagetes lucida* Cav. In this study the authors suggested that plants categorized as such are considered most effective, whereas the other plants in the complex are given secondary status.

Using results of Linares and Bye and similar studies, the staff of the Jardín Botánico has been able to implement public education programs aimed at increasing the level of botanical literacy. Each year, special weeks are set aside to focus on traditional medicine, and individual healers set up stalls in the garden to advise the public on the uses of medicinal plants. There are also special workshops on medicinal plants of Mexico geared toward those interested in alternative medicine. In addition, the garden promotes the use of edible plants of Mexican origin. One project was a series of lectures on the botany, history, culinary preparation, nutrition, and other aspects of edible greens, both wild and cultivated. The public was invited to sample these species, and a publication with botanical information and recipes was issued. The staff of the Jardín Botánico used ethnobotany to communicate important messages about biological diversity, its utilization and conservation, to the public.

Quantitative Ethnobotany

The quantification of ethnobotanical data was first undertaken in a study of the Chácabo Indians of Amazonian Bolivia (Boom, 1987). This was a major step toward a much more rigorous methodology where a statistical approach could be utilized. Ethnobotanical studies of 360 species of vascular plants known by the Chácabo identified uses for 305 species. In a one-hectare plot, 78.7% of the tree species and 95% of the individual trees were utilized. Balée continued this work among the Ka'apor and Tembé Indians of Brazil, and Boom later studied the Panare of Venezuela; the results are summarized in Table 1 (Prance et al., 1987). Their conclusions indicate a particular need for conserving plant families, such as Palmae, Lecythidaceae, Chrysobalanaceae, and Malpighiaceae, that are utilized extensively by these four indigenous groups, as well as the terra firme forest, in which most of the useful species occur. These studies were the first attempt to quantify the value of the forest to indigenous people and thus argue for its conservation based on the percentage of species used locally.

Table 1. Percentage of useful species (in all categories specified) per hectare plot to the indigenous groups studied.

Indigenous group	Percentage of useful tree species from inventory sites
Ka'apor	76.8
Tembé	61.3
Chácabo	78.7
Panare	48.6

Source: Prance et al. (1987).

Working in Tambopata, Peru, with mestizo people, Phillips and Gentry (1993a) proposed a new quantitative method for ethnobotanical studies. They studied tree plots in seven different forest types in a total of 6.1 hectares. "Family use values" were calculated for plants employed for construction, in commerce, food, technology, and medicine. Using the same data set, Phillips and Gentry (1993b) questioned whether the age of the informant had any effect on his/her knowledge of plant use. They found that in some use categories, such as medicinal plant lore, the bulk of the information is held by older people, and suggested that areas such as this should be the main thrust of ethnobotanical studies and conservation efforts. Other students in this field, such as Miguel Alexiades and Ana Irene Batis, are currently undertaking fieldwork that uses the quantitative approach in ethnobotany. It seems apparent that a quantitative approach will allow ethnobotanists to question more precisely forest inventory, economics, forest management, market studies, or other topics.

Resource Management

Caballero (1994) studied the use and management of *Sabal* Adans. (Arecaceae) among the Yuc-

atec Maya of Mexico, an example of a contemporary study of the relationship between plants and people. *Sabal* is a multi-use palm that has served as a source of construction material, firewood, food, medicine, and magic. Caballero discovered that some traditional uses of the trees had disappeared (magic, medicine), others were declining (broom making, poles, and fences), while others persisted (thatch, fuel) or increased (handicrafts). His studies showed the greatest pressure on the resource was for thatch, where some 3500–5000 *Sabal* leaves, requiring 250–1250 trees (ranging from juvenile to adult), are needed to thatch a house in the region. The importance of indigenous resource management as a way of maximizing future supplies of palm leaves is evident from this study, as are the dangers posed by overexploitation of the resource. Anderson (1988) studied *Euterpe oleracea* Mart., another palm commonly used in Amazonian Brazil, and found that a single family received U.S. $15,532.86 from sales of açai fruit (63.1% of its annual cash income), and U.S. $2,916.79, or 11.8% of its income from sales of palm heart. Because palms are so important to tropical forest dwelling people, this plant family is a primary candidate for additional resource management studies.

Pharmaceutical Prospecting

Cox (1994) estimated that at least 50 pharmaceutical drugs have been discovered from ethnobotanical leads. These include digoxin used to treat atrial fibrillation, isolated from *Digitalis purpurea* L., a plant employed in the eighteenth century to treat dropsy, an accumulation of fluid resulting from heart failure. A more recent discovery was of vincristine and vinblastine, both used to treat blood cancers, isolated from *Catharanthus roseus* (L.) G. Don, which has been used in the Caribbean to treat "sweet blood" (diabetes).

Cox's ethnobotanical research in Samoa has led to the discovery of a potent anti-viral compound, prostratin, derived from *Homalanthus nutans* Guill. Cox identified this plant in 1984, after learning about it from several healers who used it to treat yellow fever. When tested at the National Cancer Institute, an extract of this plant exhibited powerful *in vitro* activity against HIV (Gustafson et al., 1992). The National Cancer Institute is now planning to license prostratin to a drug company for additional study. Cox also identified a topical anti-inflammatory from *Erythrina variegata* L., utilized by healers in Samoa to treat skin inflammation. The active component, a flavanone, is now being developed by Shering-Plough Corporation. Cox has also worked to ensure that a significant portion of royalties earned from the sales of these compounds will be returned to the Samoan people. His foundation (Seacology Foundation) has helped raise funds to protect 64,000 acres of tropical forest by creating four village-owned and -managed reserves. Although most ethno-directed pharmacological prospecting in the past has not returned benefits to native people or helped to conserve the forest ecosystems where the source plants are found, it is clear that ethnobotanical studies such as those of Cox and his students have done much to create a new model for this type of research. A for-profit entity, Shaman Pharmaceuticals, Inc., was founded with a corporate philosophy that creates mechanisms to ensure both short- and long-term benefits to traditional people, and promotes conservation of forest ecosystems in the areas the company gathers plants through The Healing Forest Conservancy, a foundation it established and supports.

The Belize Ethnobotany Project

The Belize Ethnobotany Project was initiated in 1988 as a collaborative endeavor between the Ix Chel Tropical Research Foundation, a Belizean non-governmental organization, and the Institute of Economic Botany of The New York Botanical Garden. The principal purpose of the project has been to inventory the ethnobotanical diversity of Belize, a country with significant tracts of intact forest as well as nine different cultural and ethnic groups. Dozens of expeditions since 1988 have resulted in some 3600 collections of plant specimens, over 50% with ethnobotanical descriptions. Duplicate specimens have been deposited in the herbaria of the Belize College of Agriculture, the Belize Forestry Department, The New York Botanical Garden, and the US National Herbarium. A database maintained at The New York Botanical Garden will be distributed to several computer facilities within Belize. The Project has gathered traditional knowledge graciously provided by over two dozen traditional healers of Mopan, Yucatec, Kekchi, Maya, Ladino, Garifuna, Creole, East Indian, and Mennonite descent.

The ethnobotanical inventory has been combined with the production of an annotated checklist of the flowering plants and ferns of Belize, based on collections of the ethnobotany project, previously available herbarium specimens, and relevant literature. With the input of dozens of taxonomic specialists, the checklist will help determine the comprehensiveness of the ethnobotanical survey.

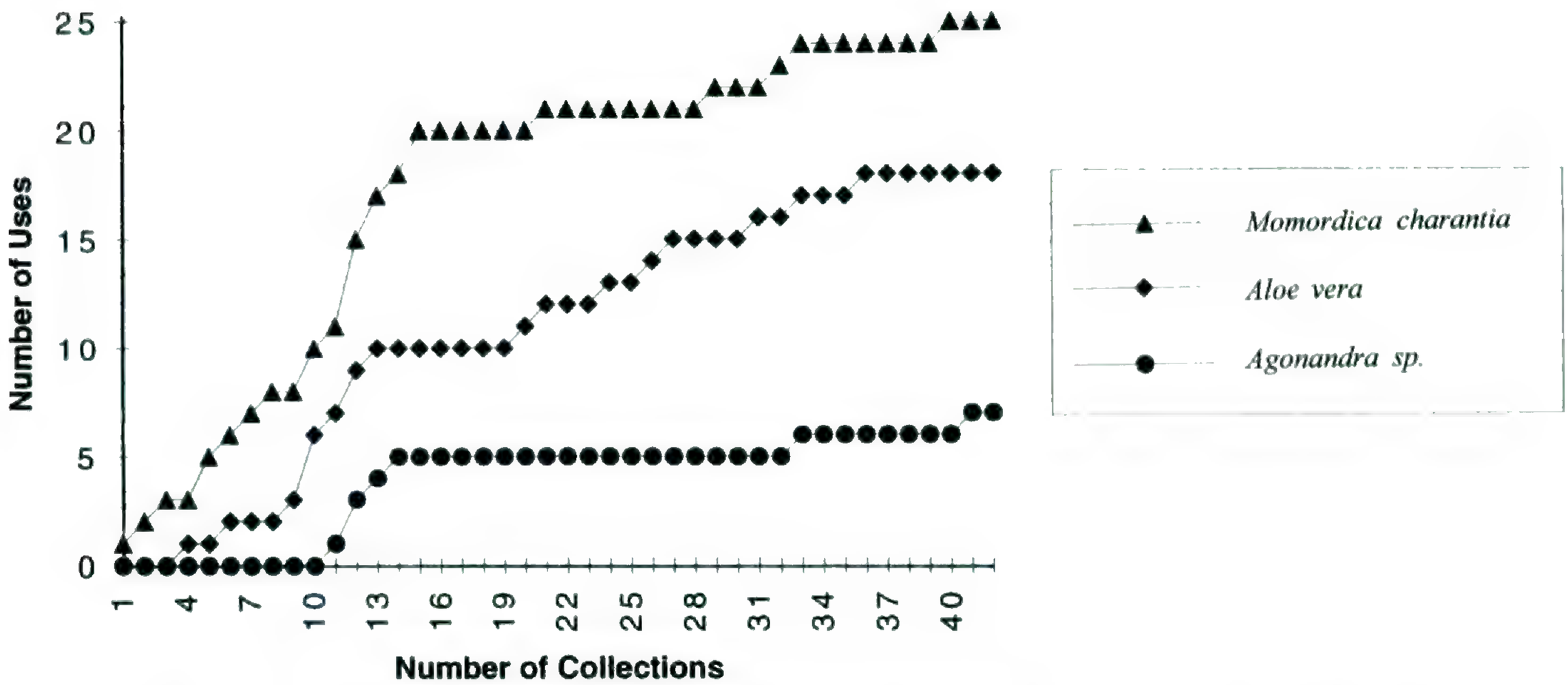

Figure 1. Graph demonstrating the importance of multiple interviews in investigating local uses of economically important plants. The Number of Collections represents the number of people interviewed and the Number of Uses, the different ways in which each species is used. With each of the species represented in this graph, new uses are still being described after interviews with as many as 40 people.

A. THE CONCEPT OF THE MULTIPLE USE CURVE

Rigorous ethnobotanical study demands accurate determination of appropriate sample size, the number of collections, and number of people interviewed, in order to ensure that the information on a specific plant is relatively complete. Many previous ethnobotanical studies have depended on one or a small number of collections as the basis for their information and conclusions. A mathematical relationship can be developed, based on the concept of the species area curve (Campbell et al., 1986), to assess the appropriate number of collections or interviews.

Figure 1 graphs the relationship between the number of different uses of three species versus the number of people interviewed, based on 42 interviews in August and September 1994. Interviewees were, for the most part, not traditional healers, but elderly people willing to discuss the uses of ten plant species. Three species have been selected to illustrate the type of knowledge obtained.

The upper curve in Figure 1 illustrates the uses of *Momordica charantia* L., a vining herb common to much of the Caribbean and elsewhere. The initial 13 interviews record 20 uses, but 5 additional uses were documented by the 39th interview. This curve illustrates a pattern for a "powerful plant" (Balick, 1990), one that is widely known with multiple uses. The middle curve is for *Aloe vera* (L.) Burm. F., a commonly known plant with a more focused series of uses, especially in the area of dermatology. The final species, *Agonandra* Miers ex Benth. sp., is an example of a plant that is not commonly known throughout the community and appears to have fewer uses, focused on "male" problems. It also has a more limited distribution in Belize than the other two taxa, primarily in forests. One point illustrated by the multiple use curve for these three plants is the large number of interviews/collections necessary to obtain the maximum amount of data. Many ethnobotanical studies, including contemporary ones that utilize statistical methods, are based on a small number of interviews/collections per species. For some plants, such as those with specialist uses, a few collections from traditional healers may be sufficient, while more widely used plants may require several dozen interviews/collections before the total extant information can be obtained.

B. VALUATION STUDIES

One method of ascertaining the value of non-timber forest products in the tropical forest is to inventory a clearly defined area and estimate the economic value of the species found there. Peters et al. (1989) were the first to document the commercial value of non-timber forest products found within a hectare of forest in the Peruvian Amazon, but they did not include medicinal plants in their inventory. This aspect was evaluated later in Belize (Balick & Mendelsohn, 1992). From two separate

Table 2. Medicinal plants harvested from a 30-year-old valley forest plot (no. 1) in Cayo, Belize.

Common name	Scientific name	Use[a]
Bejuco verde	*Agonandra racemosa* (DC.) Standl.	Sedative, laxative, "gastritis," analgesic
Calawalla	*Phlebodium decumanum* (Willd.) J. Smith	Ulcers, pain, "gastritis," chronic indigestion, high blood pressure, "cancer"
China root	*Smilax lanceolata* L.	Blood tonic, fatigue, "anemia," acid stomach, rheumatism, skin conditions
Cocomecca	*Dioscorea* sp.	Urinary tract ailments, bladder infection, stoppage of urine, kidney sluggishness and malfunction, to loosen mucus in coughs and colds, febrifuge, blood tonic
Contribo	*Aristolochia trilobata* L.	Flu, colds, constipation, fevers, stomach ache, indigestion, "gastritis," parasites

[a] Uses listed are based on disease concepts recognized in Belize, primarily of Mayan origin, that may or may not have equivalent states in Western medicine. For example, kidney sluggishness is not a condition commonly recognized by Western-trained physicians, but is a common complaint among people in this region.

plots of 30- and 50-year-old forest a total of 308.6 and 1433.6 kg per hectare (dry weight) of medicines, respectively, whose value could be judged by local market forces, was collected. Local herbal pharmacists and healers purchase and process medicinal plants from herb gatherers and small farmers for an average price of U.S. $2.80 per kg, suggesting that harvesting the medicinal plants from a hectare would yield the collector between $864 and $4014 of gross revenue. Subtracting the costs required to harvest, process, and ship the plants, the net revenue from clearing a hectare was calculated to be $564 and $3054 on each of the two plots (Balick & Mendelsohn, 1992). The lists of plants and their uses are presented in Tables 2 and 3.

Not enough information is available to understand the life cycle and regeneration time needed for each species, thus we cannot comment on the frequency and extent of collection involved in sustainable harvest. However, assuming the current age of the forest in each plot as a rotation length, we calculated an estimate of the present value of harvesting plants sustainably into the future using the standard Faustman formula: $V=R/(1-e^{-rt})$, where R is the net revenue from a single harvest and r is the real interest rate; t is the length of the rotation in years. Given a 30-year rotation in plot 1, the present value of medicine is $726 per hectare. A similar calculation for plot 2, with a 50-year rotation, yielded a present value of $3327 per hectare. These calculations assume a 5% interest rate.

These estimates for the harvest of medicinal plants compare favorably with alternative land uses in the region, such as milpa (corn, bean, and squash cultivation) in Guatemalan rainforest, which yielded $288 per hectare. Other commercial products, such as allspice, copal, chicle, and construction materials, in the plots could be harvested and

Table 3. Medicinal plants harvested from a 50-year-old ridge, forest plot (no. 2) in Cayo, Belize.

Common name	Scientific name	Use
Negrito	*Simaruba glauca* DC.	Dysentery & diarrhea, dysmenorrhea, skin conditions, stomach and bowel tonic
Gumbolimbo	*Bursera simaruba* (L.) Sarg.	Antipruritic, stomach cramps, kidney infections, diuretic
China root	*Smilax lanceolata* L.	Blood tonic, fatigue, "anemia," acid stomach, rheumatism, skin conditions
Cocomecca	*Dioscorea* sp.	Urinary tract ailments, bladder infection, stoppage of urine, kidney sluggishness and malfunction, to loosen mucus in coughs and colds, febrifuge, blood tonic

added to the total value of the medicinal plants. Thus, this study suggested that protection of some areas of rainforest as extractive reserves for medicinal plants appears to be economically justified. It seems that a periodic harvest strategy is a realistic and sustainable method of utilizing the forest. Based on our evaluation of forest similar to the second, 50-hectare plot analyzed, it would appear that one could harvest and clear one hectare per year indefinitely, assuming that all of the species found in each plot would regenerate at similar rates. More than likely, however, some species, such as *Bursera simaruba* (L.) Sarg., would become more dominant in the forest ecosystem, while others, such as *Dioscorea* L., could become rare.

This analysis is based on current market data, and estimates of the worth of the forest could change with local market forces. For example, if knowledge about tropical herbal medicines becomes more widespread and their collection increases, prices for source plants would fall. Similarly, if more consumers became aware of the potential of some of these medicines, or if the cost of commercially produced pharmaceuticals became too great, demand for herbal medicines could increase, substantially driving up prices. Finally, destruction of the tropical forest habitats of many of these important plants could increase their scarcity, driving up local prices. This scenario has already been observed in Belize with some species, indicating that the value of tropical forest for the harvest of non-timber forest products will increase relative to other land uses over time, as these forests become more scarce.

C. DEVELOPMENT OF A FOREST-BASED TRADITIONAL MEDICINE INDUSTRY

One of the primary dilemmas in the development of an extraction program for non-timber forest products has been the long history of overcollecting and resultant decline of resources, and export and processing of raw materials at centers and countries far from their origin. Rattan is a classic example of people in producing countries, who are closest to the resource, receiving the smallest percentage of the profits derived from its manufacture into high-quality furniture (Dransfield & Manokaran, 1993). In Central America, as elsewhere in the developing world, locally developed brands of plant-derived medicine are now being marketed with a value-added component (production and packaging) remaining in the country of origin of the raw material. As more of these products appear, based on the success of the original endeavors, greater demand for ingredients from rainforest species will result. This could contribute to preservation of tropical forest ecosystems, but only *if* people carefully manage the production or extraction of the plant species that are primary ingredients in these products. In addition to using methods of sustainable extraction from natural ecosystems, small farmers will cultivate some species for sale to both local herbalists and commercial companies. To address the latter possibility, our work in the Belize Ethnobotany Project has included a program with the Belize College of Agriculture (BCA), Central Farms, to learn how to propagate and grow over 24 different plants currently utilized in traditional medicine. Hugh O'Brien, Professor of Horticulture at BCA, has coordinated this effort, which has included the genera *Achras* L., *Aristolochia* L., *Brosimum* Sw., *Bursera* Jacq. ex L., *Cedrela* P. Browne, *Croton* L., *Jatropha* L., *Myroxylon* L.f., *Neurolaena* R. Br., *Piscidia* L., *Psidium* L., *Senna* Miller, *Simarouba* Aublet, *Smilax* L., *Stachytarpheta* Vahl., and *Swietenia* Jacq.

D. ESTABLISHMENT OF AN ETHNO-BIOMEDICAL FOREST RESERVE

The concept of the extractive reserve as a tool for conservation has received a great deal of attention over the last few years. Many of these reserves are tracts of forest where non-timber products can be harvested by local individuals or groups who theoretically have a stake in the preservation of the forest's biological integrity (Allegretti, 1990). Products such as rubber, Brazil nuts, copal resin, plant oils, fruits, fiber, construction materials, foliage and house plants for the florist trade, and other items have been selected for harvest and marketing from extractive reserves in the Amazon, Central America, Asia, and Africa. Numerous perspectives on these resources, both positive and negative, have been highlighted recently (Browder, 1992; Ryan, 1991).

In June 1993, a 6000-acre, lowland tropical forest, government-owned reserve was established for the extraction of medicinal plants, teaching, and apprenticeship, with financial support from The Healing Forest Conservancy and The Rex Foundation. This particular forest, in the Yalbak region of Belize, contains a broad diversity of medicinal plant species. Also within its borders are many species of animals, including jaguar, tapir, peccary, howler monkeys, and numerous other mammals, birds, and reptiles.

A unique feature of this reserve is that it has been designated for the extraction of medicinal plants used locally as part of the primary health

Table 4. Credibility rating for use information collected.

Category	Rating	Hypothetical example
Collector uses or directly observed use	1	Dr. Smith saw these *Orbignya cohune* leaves being used as thatch in Belize.
Informant uses or directly observed use	2	Maya healer, Don Elijio, told Dr. Smith he uses these *Piper amalago* roots for snakebite.
Informant heard/knew from a further source	3	Ethnographer on the Sioux reservation heard that the Sioux used the *Aster* for menstruation problems.
Use reported from the literature	4	As for the IEB teaching collection, where uses will be gathered from the literature and summarized on the use label.
Common knowledge	5	As, for example, a collection of a cultivar of coffee from a coffee plantation with a reported use as a stimulant beverage.
Credibility of use information unknown	6	New field botanist neglected to write down any information about his informant.

care network. Accordingly, this type of extractive reserve was classified as an "ethno-biomedical forest reserve" (Balick et al., 1994), a term intended to convey a sense of the interaction between people, plants, and animals, and the health care system in the region.

One objective of the reserve is ethnobotanical and ecological research, designed to identify the plant resources it contains and develop appropriate technologies for their sustainable extraction. David Campbell and his students from Grinnell College (Iowa, U.S.A.) have constructed ecological transects in selected parts of the reserve to serve as long-term study sites. Some of these transects will monitor extraction, while others monitor changes in the native vegetation. Ethnobotanical inventories have begun to catalog economically important plants in the reserve, as well as in the surrounding Cayo District. Other scientists will be invited to participate in these studies.

It will be many years before this first ethno-biomedical forest reserve can be judged a success or failure. A great deal of work must go into developing the management plan and finding the financial and human resources to implement it. Land use pressures surrounding the reserve, specifically logging and agriculture, as well as sociological and political factors, could endanger the long-term existence of the reserve. However, in Belize there is a great deal of optimism and support, much of it at the grass roots level. Reserves for protecting medicinal plants recently have been established across India, in a nationwide effort to ensure the supply of these important species.

Conclusion

The discipline of ethnobotany is currently evolving both in its philosophical underpinnings and methodology. Contemporary studies are incorporating the most powerful techniques of molecular pharmacology and computerization in the analysis of ethnobotanical data. One recent development being implemented at The New York Botanical Garden's (NYBG) Institute of Economic Botany (IEB) is the establishment of a "credibility rating" for information that is collected on plant utilization. In the past there was little opportunity to evaluate the quality of data based on the way it was collected during ethnobotanical studies. When extracting information from the ethnobotanical literature, it is rarely clear whether the investigator actually observed or participated in the uses discussed, or whether the data were collected during a casual walk through the forest with a younger person who remembers specific uses of the plants by one of his forebears. To address this, the credibility rating presented in Table 4 will be incorporated into the database at NYBG. Data with a rating of 1 have a reasonable certainty of being accurate, while those with a rating of 5 or 6 may be less authoritative. Although this rating is an experiment, and will certainly be revised over time, it is an attempt to begin to standardize the quality of data collected and evaluate its relative credibility.

There is a deep, often spiritual relationship between plants and people, in both traditional settings and among more acculturated societies. These relationships can be elucidated through ethnobotanical studies and used to increase biological literacy among the non-scientific community, as evidenced by work in Mexico, Samoa, and Belize. If the most crucial issues of biodiversity conservation are to be addressed successfully, we need to improve the educational system's ability to communicate the importance of science, not only to people in the Unit-

ed States but around the world. It is essential to build on the value of systematic knowledge and link it with the world in a way that inspires the largest possible constituency to appreciate the importance of biodiversity and the need for its conservation. Ethnobotany has been an important tool for meeting this goal, and will continue to be in the future. In the context of Systematics Agenda 2000, it is worth recalling the words of Ralph Waldo Emerson who wrote, "Nature tells every secret once." It is imperative that we heed these words and become better prepared to understand those secrets.

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THE *PROSOECA PERINGUEYI* (DIPTERA: NEMESTRINIDAE) POLLINATION GUILD IN SOUTHERN AFRICA: LONG-TONGUED FLIES AND THEIR TUBULAR FLOWERS[1]

John C. Manning[2] *and Peter Goldblatt*[3]

ABSTRACT

A guild of 28 winter- and spring-flowering species of two plant families, Iridaceae and Geraniaceae, with intense purple to crimson flowers and extremely long and slender perianth tubes, is pollinated exclusively by two long-tongued flies of the family Nemestrinidae. The two species of flies, *Prosoeca peringueyi* and *P. sp. nov.*, are active in the late winter and spring, have large bodies, mouthparts 20–50 mm long, and forage for nectar while hovering. Plants pollinated by these two flies share a suite of convergent floral characteristics, including a straight or slightly curved floral tube at least 20 mm and up to 70 mm long, relatively short petals or tepals colored predominantly dark blue- or red-purple with pale nectar guides, and anthers and stigmas exserted from the tube and usually unilateral in orientation. With one exception, the flowers of all species secrete large amounts of nectar of relatively constant total sugar concentration, mostly 24–29%, and high sucrose:hexose ratio. Most members of the guild have odorless flowers. The long floral tube makes nectar unavailable to most insects, including a variety of bees, wasps, and other flies that pollinate plants which co-occur with members of the long-tubed flower guild. The two *Prosoeca* species have mouthparts long enough to forage effectively on these long-tubed flowers, and they are also effective pollinators because pollen adheres to their bodies and is transported from flower to flower. The flies visit a wide range of plants but are effective pollinators only of those with tube lengths greater that their proboscis lengths. We have identified four mutually exclusive sites of pollen deposition on the insects' bodies: when two or more members of the guild co-occur, each species typically utilizes a different pollen deposition site. This suggests that pollen contamination is detrimental to reproductive success. Differential pollen deposition sites may have evolved in response to selection for reduced pollen contamination. Since 27 of the 28 plant species appear to depend exclusively on these two species of *Prosoeca* for pollination, these flies must be considered keystone species in the ecosystems where they occur.

A close association between the form and color of flowers and pollination by a particular pollinator is well known. Convergence in floral morphology among species that rely on the same pollinator class led to the recognition of floral syndromes (Faegri & van der Pijl, 1979; Grant, 1981; Vogel, 1954). Those species with morphologically similar flowers that share the same pollinator species constitute a particular pollination guild, an extension of the term (Root, 1967) describing a group of species that exploits the same class of resources in a similar way. A guild is thus a functional unit independent of taxonomic considerations. Although a number of pollination syndromes have been identified in the southern African flora (Vogel, 1954), very few guilds have been described. The most striking of those that have been documented is the association between the butterfly, *Aeropetes* (*Meneris*) *tulbaghia*, and late summer-flowering plant species with large bright red blossoms (Johnson & Bond, 1994).

Pollination by long-tongued flies is a relatively unusual phenomenon, first documented in southern Africa by Rudolf Marloth (1908) and later in somewhat more detail by Stefan Vogel (1954). Although pollination by long-tongued flies has also been reported in India (Fletcher & Son, 1931) and California (Grant & Grant, 1965), it appears to be particularly well developed only in southern Africa.

In the western part of southern Africa 28 species of Iridaceae and Geraniaceae have intensely colored purple to crimson flowers with extremely long floral tubes. These species all occur in a restricted geographic area, flower between July and September, and often occupy similar habitats. The conver-

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gent floral morphology in this group of spring-flowering geophytes and small shrubs constitutes a distinct floral syndrome, and their coincident geography and phenology suggests that they are members of a specific pollination guild. Some of these species belong to the genus *Lapeirousia* (Iridaceae) and have already been found to be pollinated by one or both of two species of long-tongued flies in the genus *Prosoeca* (Diptera:Nemestrinidae) (Goldblatt et al., 1995). The purpose of this investigation is to extend our observations to determine whether the convergence in floral morphology to the *L. silenoides*-type flower in the other species coincides with pollination by the same fly species. Our results support the recognition of a distinct pollination guild. We discuss some of the implications of such a specialized pollination system on plant ecology and evolution and consider its possible origin.

Methods

Plant species

Members of the guild were initially identified during the course of field research in 1992 and 1993 in connection with a study of pollination ecology of *Lapeirousia* subg. *Lapeirousia* (Goldblatt et al., 1995). In this study species with purple to crimson flowers, white to cream nectar guides, and a perianth tube in excess of 30 mm were pollinated by *Prosoeca peringueyi* or *P. sp. nov.*, or occasionally both. We then reviewed the literature for records of species with purple to crimson flowers recorded from the west coast of southern Africa. All species having a perianth tube at least 30 mm long, or the anthers and stigmas held at least 30 mm from the base of the floral tube, were listed for further study. These species were examined in the field whenever possible to obtain observations on nectar characteristics and pollinators (Table 1). The apparent floral tube length was determined as the distance from base to the mouth of the tube. The actual floral tube length is less in some species due to the occlusion of the lower part of the tube and was determined empirically as the level down to which nectar could be freely extracted using a micropipette. Functional tube length was determined as actual tube length plus the distance between the mouth of the tube and the mid point of the anthers. Measurements were made on a minimum of 10 individuals per population.

Complete distribution ranges of plant species were taken from the literature and supplemented by recent herbarium records. Voucher specimens were made for all populations studied. Plant vouchers are deposited at the Missouri Botanical Garden Herbarium, St. Louis (MO), and the Compton Herbarium, Cape Town (NBG).

Insect species

Observations of insect foraging (Figs. 1–6) involved 4–20 hours per species and included such aspects as the density and diversity of floral foragers and how they removed rewards from flowers. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Location of pollen deposits was based first on visual observation of foraging insects and later on examination of pinned specimens. Individual insects were washed of pollen after pinning by placing the insect on a glass slide and rinsing the whole body in 100% ethanol while gently dislodging pollen loads on the frons, thorax, and sternum with a dissecting needle. The dry pollen residue was stained and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). To prevent contamination of the body of an insect with pollen carried by another in the same jar, the bodies of insect specimens were isolated from each other by wrapping them in tissue. Insect distributions were determined from collections at the Natal Museum, Pietermaritzburg, and the South African Museum, Cape Town, plus our own observations and collections. Insect vouchers are deposited at the Natal Museum, Pietermaritzburg.

Nectar analyses

Nectar volume measurements (Table 2) were made from unbagged flowers in the field and represent the standing crop that will be influenced by visitation rates. Whole flowers were picked and nectar was withdrawn from the base of the floral tube with 3 µl capillary tubes after separating the ovary from the perianth (Iridaceae) or base of the hypanthium tube from the pedicel (Geraniaceae). Nectar was extracted from five or more individuals per population in most cases (Table 2). Nectar samples were dried on Whatmans filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for analysis (Table 2). The percentage of sucrose equivalents in fresh nectar was measured in the field on a Bellingham & Stanley handheld refractometer (0–50%) from five or more individuals per population.

Results

Plant characteristics

A total of 28 plant species occurring along the west coast and near interior of southern Africa, and

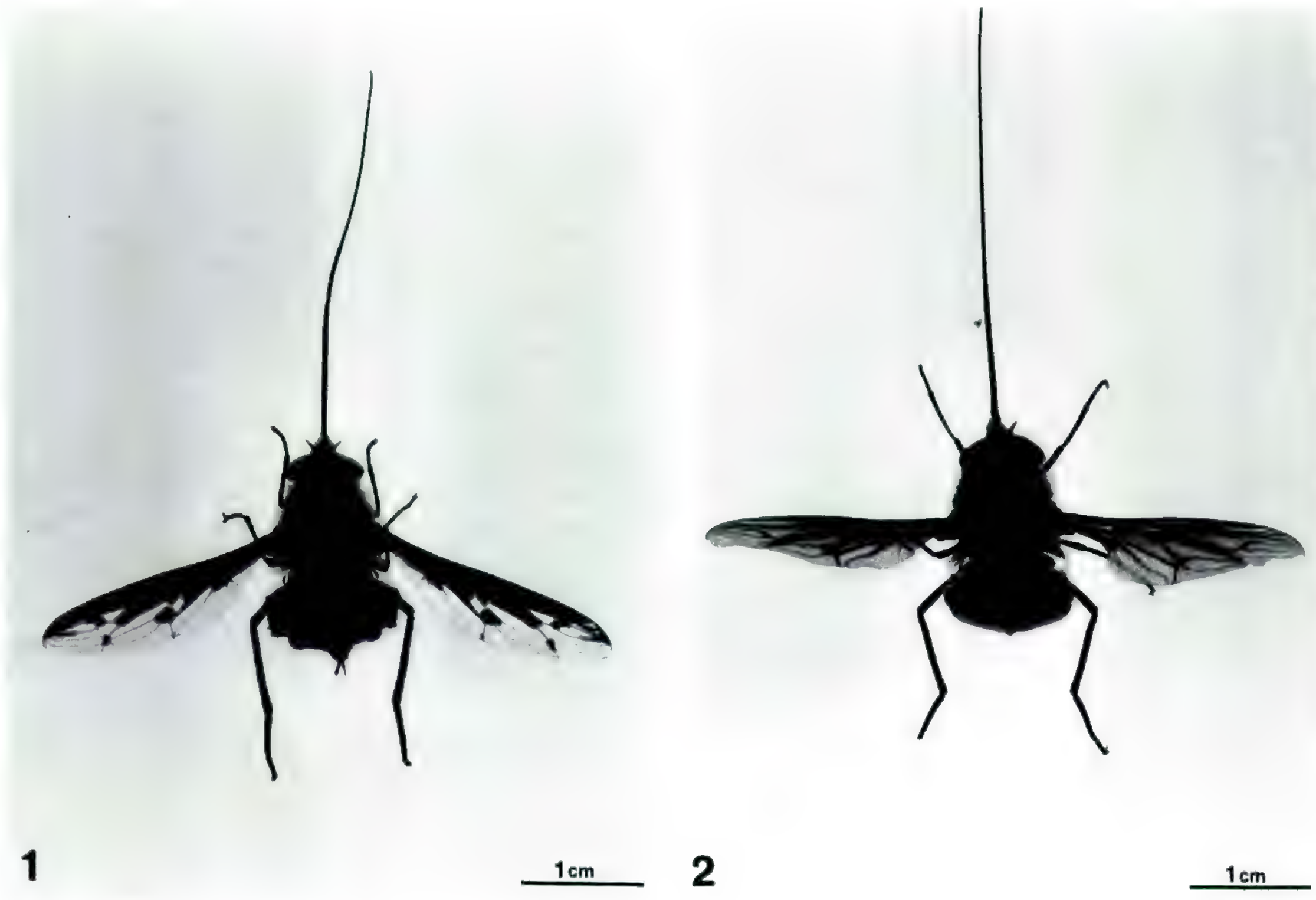
Table 1. Species belonging to the *Prosoeca peringueyi-P. sp.* pollination guild. Pollinators in parentheses are inferred on the basis of geography and pollinators of co-occurring plant species (*P. peringueyi* and *P. sp.* are not sympatric). Study sites and dates of observations on pollinators are listed for those species for which pollinator observations are available.

Family/species	Pollinator	Study site
Geraniaceae		
Pelargonium		
cortusifolium L'Herit.	(*P. peringueyi*)	
crassicaule L'Herit.	(*P. peringueyi*)	
echinatum Curt. (purple-flowered form)	(*P. peringueyi*)	
incrassatum (Andr.) Sims	*P. peringueyi*	Steinkopf-Anenous Pass (24 Aug. 1992); Kamieskroon (24 Aug. 1993); Garies Hill (23 Aug. 1994); Spektakel Mts. (5 Sep. 1994); Kamiesberg, Leliefontein (13 Sep. 1993 and 20 Sep. 1994)
magenteum van der Walt	*P. peringueyi*	Bidouw Valley (12 Aug. 1994)
sericifolium van der Walt	*P. peringueyi*	Steinkopf-Anenous Pass (24 Aug. 1992)
Iridaceae		
Babiana		
curviscapa G. Lewis	*P. peringueyi*	Spektakel-Naries (4 Sep. 1994)
dregei Baker	*P. peringueyi*	Kamiesberg, Sneeukop (12 Sep. 1993); Kamiesberg, Leliefontein (13 Sep. 1993 and 20 Sep. 1994)
ecklonii Klatt	(*P. peringueyi*)	—
flabellifolia Harv. ex Klatt	*P. sp. nov.*	Hantamsberg Plateau (3 Sep. 1994)
framesii L. Bolus	*P. peringueyi*	Oorlogskloof Nature Reserve (8 Sep. 1993)
	P. sp. nov.	Nieuwoudtville Nature Reserve (8 Sep. 1992 and 4 Sep. 1994)
geniculata G. Lewis	(*P. peringueyi*)	—
pubescens G. Lewis	*P. peringueyi*	Garies Hill (23 Aug. 1994)
sambucina var.		
longibracteata G. Lewis	(*P. sp.*)	—
unguiculata G. Lewis	(*P. peringueyi*)	—
Geissorhiza		
kamiesmontana Goldblatt	(*P. peringueyi*)	—
Hesperantha		
latifolia (Klatt) de Vos	*P. peringueyi*	Kamiesberg, Sneeukop (12 Sep. 1993)
oligantha Diels	(*P. sp.*)	—
purpurea Goldblatt	(*P. peringueyi*)	—
Lapeirousia		
dolomitica subsp.		
dolomitica Dinter	*P. peringueyi*	Anenous Hills (24 Aug. 1992)
lewisiana (B. Nord.) Goldblatt	(*P. peringueyi*)	—
jacquinii N. E. Br.	*P. sp. nov.*	Oorlogskloof Farm (8 Sep. 1992); Oorlogskloof Nature Reserve (8 Sep. 1992)
	P. peringueyi	Botterkloof Pass (23 Aug. 1993); Farm Alpha (1 Sep. 1994)
oreogena Schltr.	*P. sp. nov.*	Glenlyon (23 Aug. 1993 and 4 Sep. 1994); Nieuwoudtville Nature Reserve (4 Sep. 1994)
pyramidalis subsp. *regalis* Goldblatt & J. Manning	*P. peringueyi*	Trawal (5 and 11 Aug. 1994)
silenoides (Jacq.) Ker-Gawl.	*P. peringueyi*	Spektakel Pass (23 Aug. 1992); Kamieskroon to Grootvlei (22 Aug. 1992); Kamieskroon (2 Aug. 1993); 10 km S Kamieskroon (24 Aug. 1993); Garies Hill (23 Aug. 1994)
violacea Goldblatt	*P. peringueyi*	Botterkloof Pass (23 Aug. 1993)

Table 1. Continued.

Family/species	Pollinator	Study site
Romulea		
hantamensis (Diels) Goldblatt	*P. sp. nov.*	Hantamsberg (3 Sep. 1994)
Sparaxis		
variegata subsp. *metelerkampiae* (L. Bolus) Goldblatt	*P. peringueyi*	Pakhuis Mts., Farm Alpha (1 Sep. 1994)
Tritonia		
marlothii de Vos	(*P. peringueyi*)	—
Xenoscapa		
uliginosa Goldblatt & J. Manning	(*P. peringueyi*)	—

mostly endemic there, were identified as converging on *Lapeirousia silenoides* in floral morphology (Table 3). These include 22 species of Iridaceae in the genera *Babiana, Geissorhiza, Hesperantha, Lapeirousia, Romulea, Sparaxis, Tritonia,* and *Xenoscapa,* and six species of Geraniaceae, all in the genus *Pelargonium.* Within this group are seasonal geophytes (Iridaceae and *Pelargonium incrassatum*) and small to moderate-sized shrubs (*Pelargonium cortusifolium, P. crassicaule, P. echinatum, P. magenteum,* and *P. sericifolium*). While the habits and growth forms of the species vary, their flowers share several unusual properties and may be considered to constitute a distinct floral syndrome (Figs. 7–9). The floral tube is straight or slightly curved to sigmoid, very narrow (1.5–2.5 mm diam.), and (18–) 30–70 mm long, and the petals or tepals are shorter than the tube. The flowers are typically zygomorphic, with stamens and styles unilateral, but are actinomorphic in five species in which the stamens are sym-



Figures 1, 2. The *Prosoeca* species responsible for pollinating plant species with the *Lapeirousia silenoides*-type flower.—1. *P. peringueyi.*—2. *P. sp. nov.*

Figures 3–6. *Prosoeca* species foraging on *Lapeirousia silenoides*-type flowers. In these photographs the flies are inserting their mouthparts into the floral tubes and have not yet probed deep enough to reach the nectar in the lower part of the tube or brush the anthers and stigmas of the flowers.—3. *P. peringueyi* visiting *L. pyramidalis* subsp. *regalis*.—4. *P. peringueyi* visiting *Babiana dregei*.—5. *P. peringueyi* and *L. silenoides*.—6. *P. sp. nov.* and *L. oreogena*.

Table 2. Nectar characteristics of species with the *Lapeirousia silenoides*-type flower. Fru = fructose, Glu = glucose, Suc = sucrose. Sample size for nectar volume figures are indicated in parentheses in volume column; sample size for nectar sugar components is in the last column after sucrose:fructose + glucose ratio.

Family/species	Volume µl (n)	Mean % sugar	Fru	Glu	Suc	Mean Suc/ Glu + Fru (n)
Geraniaceae						
Pelargonium						
cortusifolium	2.6–3.1 (2)	24	—	—	—	—
incrassatum	1.5–2.2 (1)	38	0	75	25	0.33 (1)
magenteum	0.6–1.8 (5)	29	38	40	22	0.28 (1)
sericifolium	no measurable nectar produced					
Iridaceae						
Babiana						
curviscapa	2.0–4.4 (5)	25	12	19	69	2.23 (1)
dregei	3.9–9.6 (5)	22	13–15	19–21	64–68	1.94 (2)
ecklonii	4.3–8.9 (5)	27.7	5–11	10–18	72–85	3.29 (3)
flabellifolia	3.9–9.6 (5)	27	7	14	79	3.76 (1)
framesii	2.6–6.4 (5)	26	7–9	12–14	77–81	3.84 (3)
geniculata	3.2–4.8 (5)	29	17	21	62	1.63 (1)
pubescens	3.2–4.8 (5)	28	3–8	9–14	78–88	2.18 (2)
sambucina						
var. *longibracteata*	3.9–6.6 (3)	30	6–12	10–19	69–84	3.48 (3)
Hesperantha						
latifolia	0.7–1.1 (10)	24	23–29	24–30	41–53	0.94 (3)
oligantha	1.1–1.8 (5)	26.4	19–23	24–25	52–57	1.20 (2)
Lapeirousia						
dolomitica						
subsp. *dolomitica*	1.4–5.5 (5)	29	4–9	12–14	77–84	4.13 (2)
subsp. *lewisiana*	5.1–5.5 (4)	27	5–12	14–25	63–81	2.94 (5)
jacquinii	1.5–2.3 (6)	26	8	17	75	3.00 (1)
oreogena	2.5–7.3 (10)	26	13	21.5	65.5	1.90 (4)
pyramidalis						
subsp. *regalis*	2.6–4.8 (10)	28	4–21	12–31	48–84	2.45 (6)
silenoides	1.7–3.6 (16)	27	5–8	18–27	65–77	2.45 (3)
violacea	1.4–1.8 (10)	27	9–13	15–16	71–76	2.77 (2)
Romulea						
hantamensis	3.7–5.2 (3)	20	23	27	50	1.00 (1)
Sparaxis						
variegata subsp.						
metelerkampiae	1.7–2.2 (6)	28.5	1–12	4–22	70–95	3.23 (4)
Tritonia						
marlothii	1.8–3.5 (5)	29	13–14	17–18	68–70	2.23 (2)

metrically arranged around a central style (Table 3). In all species except *Pelargonium sericifolium* (which does not produce nectar; Goldblatt et al., 1995), nectar accumulates at the base of the floral tube and fills its lower third. Nectar is thus accessible only to insects with tongues long enough to reach at least into the lower third of the tube.

The flowers are mostly intensely pigmented in colors ranging from dark blue-purple and violet to bright red-purple or cerise, but are pale mauve in taxa from the Richtersveld (northern Namaqualand) and southern Namibia. Contrasting markings in white or cream are almost always present, usually accompanied by additional darker areas of pigmentation (Figs. 7–9). The markings, which may take the form of streaks or spots near the tepal bases in species of Iridaceae, are confined to the lower tepals in species with zygomorphic flowers but are present on all the tepals in species with actinomorphic flowers. In *Pelargonium* (Fig. 7) the pale color signal is provided by the white filaments, which are unilateral and declinate, rather than by tepal coloring. Whatever the shape and color of the flowers, the anthers and stigmatic surfaces are always held outside the mouth of the floral tube in a position where they will be brushed by the body of an insect probing the

Table 3. Floral characteristics of species with the *Lapeirousia silenoides*-type flower. The floral tube is closed in the lower 10–12 mm in *B. curviscapa*, 20–30 mm in *B. dregei*, and 15–20 mm in *B. framesii*, hence floral tube length does not reflect the distance that an insect must extend its mouthparts to reach the nectar. Z = zygomorphic; A = actinomorphic.

Family/species	Symmetry	Scent	Tube length (mm)	Flowering time
Geraniaceae				
Pelargonium				
cortusifolium	Z	0	ca. 30	Mar.–Nov.
crassicaule	Z	0	15–25	(Mar.–)Aug.–Sep.(–Oct.)
echinatum	Z	0	25–55	(July–)Aug.–Oct.
incrassatum	Z	0	30–40	Aug.–Sep.
magenteum	Z	0	33–47	(June–)July–Sep.
sericifolium	Z	0	35–60	(July–)Aug.–Sep.
Iridaceae				
Babiana				
curviscapa	Z	0	36–48	Aug.–Sep.
dregei	Z	0	50–65	Aug.–Sep.
ecklonii	Z	0	40–50	Sep.
flabellifolia	Z	0	40–65	Aug.–Sep.
framesii	Z	1	60–70	Aug.–Sep.
geniculata	Z	0	35–45	Aug.
pubescens	Z	0	ca. 50	(July–)Aug.
sambucina				
var. *longibracteata*	Z	1	30–50	Aug.–Sep.
var. *unguiculata*	Z	1	38–55	Aug.–Sep.
Geissorhiza				
kamiesmontana	Z	0	18–25	Sep.
Hesperantha				
latifolia	A	0	15–25	Aug.–Sep.
oligantha	A	0	30–36	Sep.(–Oct.)
purpurea	A	0	ca. 20	Sep.
Lapeirousia				
dolomitica				
subsp. *dolomitica*	Z	1	25–45	(June–)July–Sep.
subsp. *lewisiana*	Z	0	45–55	July–Aug.
jacquinii	Z	0	30–40	July–Sep.
oreogena	A	0	50–60	Aug.(–Sep.)
pyramidalis				
subsp. *regalis*	Z	0	40–50	July–Aug.
silenoides	Z	0	40–55	July–Sep.
violacea	Z	0	35–40	Aug.–Sep.
Romulea				
hantamensis	A	0	50–70	Aug.–Sep.
Sparaxis				
variegata				
subsp. *metelerkampiae*	Z	0	34–37	Aug.–Sep.
Tritonia				
marlothii	Z	0	25–44	Aug.–Sep.
Xenoscapa				
uliginosa	Z	0	25–30	Sep.(–Oct.)

tube. Pollen is often inconspicuous and of the same color as the tepals, especially in *Lapeirousia*, or may be white, possibly adding to the signal provided by the contrasting color of the perianth. In *P. incrassatum* and *P. magenteum* the pollen is bright orange. We have no data on ultra-violet light reflectance in any of the species under consideration; and it is possible that differential reflectance in the UV light range may add to the visual signals evident in the visible range.

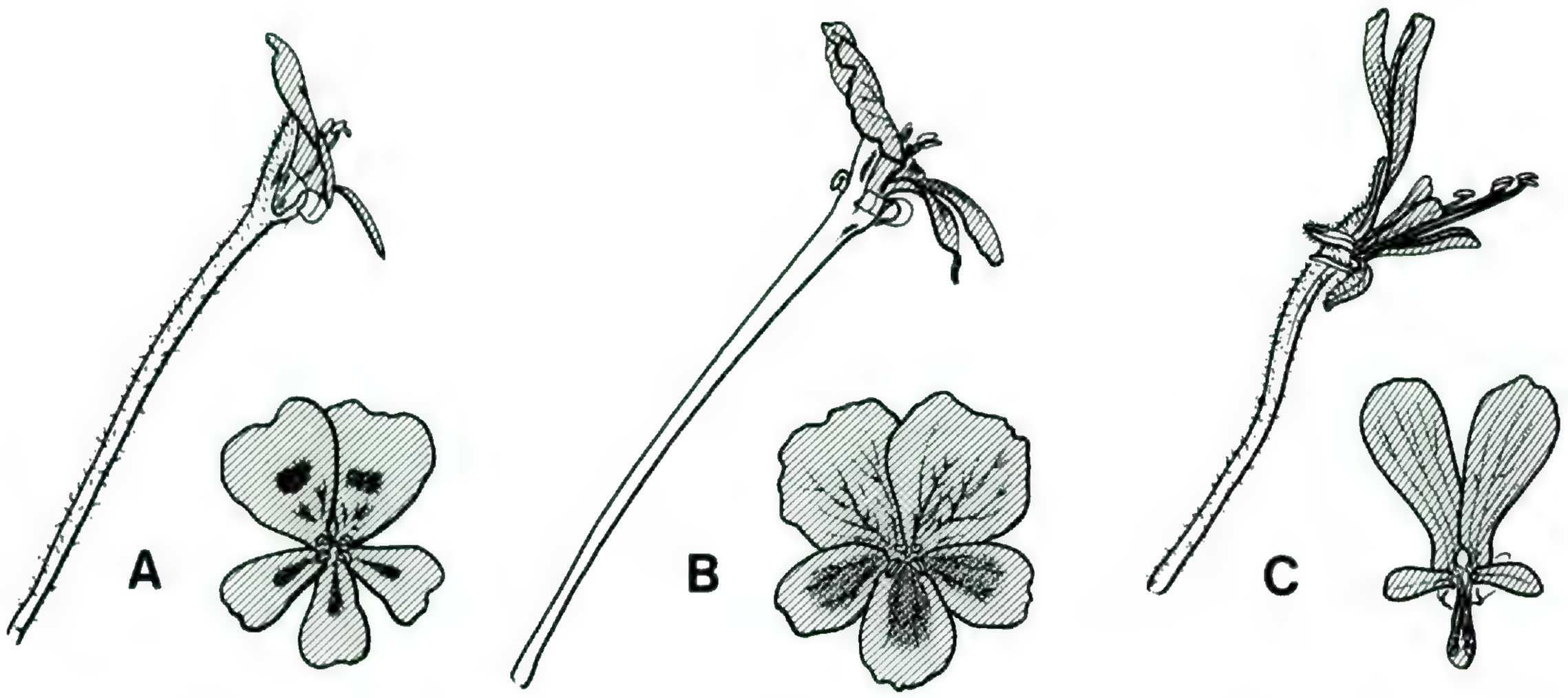


Figure 7. Flowers of species of Geraniaceae belonging to the *Lapeirousia silenoides* guild, all pollinated by *Prosoeca peringueyi.*—A. *Pelargonium magenteum.*—B. *P. sericifolium.*—C. *P. incrassatum.* (Scale: full size.)

Flowers open during the day and often close partially or fully at night. They are typically unscented, at least to the human nose both in the open air and when several flowers are held in a warm confined space. Some species of *Babiana,* however, have a light to moderately strong scent (Table 3). The flowering season in the guild ranges from late May (one species), with a marked rise in July and a peak in early September, and continues until early October (Fig. 10). Individual species and populations remain in flower for at least two weeks, or for a considerably longer time in the case of the shrubby *Pelargonium* species. Individual flowers usually last three to four days, and longer in species of Iridaceae when not pollinated. Species of Iridaceae are protandrous. The pollen is shed half a day to one day before the stigmas unfold and become available for pollen deposition. Unless removed by some agent, the pollen remains in place in the anther thecae. Species of *Pelargonium* are also protandrous. The deciduous anthers are shed the same day that the flower opens, whereas the stigmas only unfold the following day. Flowers of the species of the guild are almost all herkogamous (and self-incompatible, at least in *L. dolomitica* and *L. silenoides*) and thus require insect-mediated pollination. The only known exception is *L. jacquinii,* which is self-compatible and autogamous (Goldblatt et al., 1995).

Nectar quantities are ample, and the upper range of nectar volumes for species in the guild is 1.1 μl to 9.6 μl (Table 2). Nectar sugar concentrations are mostly 24–30%, exceptionally as low as 20% in *Romulea hantamensis* and 22% in *Babiana dregei* (Table 2). Nectar sugar analyses, available for 21 species (Table 2), show a characteristic sucrose-rich to sucrose-dominant pattern in the 15 species of Iridaceae examined. Sucrose : hexose sugar ratios range from a high of 4.13 in *Lapeirousia dolomitica* subsp. *dolomitica* to 1.20 and 0.94 in the two species of *Hesperantha* for which we have data, and 1.00 in *Romulea hantamensis,* the only species of that genus belonging to the guild. Most species have sucrose : hexose ratios in the 2 to 3.5 range. The pattern in two species of *Pelargonium,* however, shows hexose dominance with sucrose : hexose ratios of 0.28 and 0.33. This is a marked contrast to the spectrum for Iridaceae.

POLLINATOR IDENTITY

Pollinator observations were obtained for 17 out of the total listing of 28 plant species (Table 4). These species are from throughout the range occupied by members of the guild. In all of these instances pollination was carried out by either *Prosoeca peringueyi* or *P. sp.*, or, rarely, both (Figs. 1, 2). No other insects were seen to visit any of the

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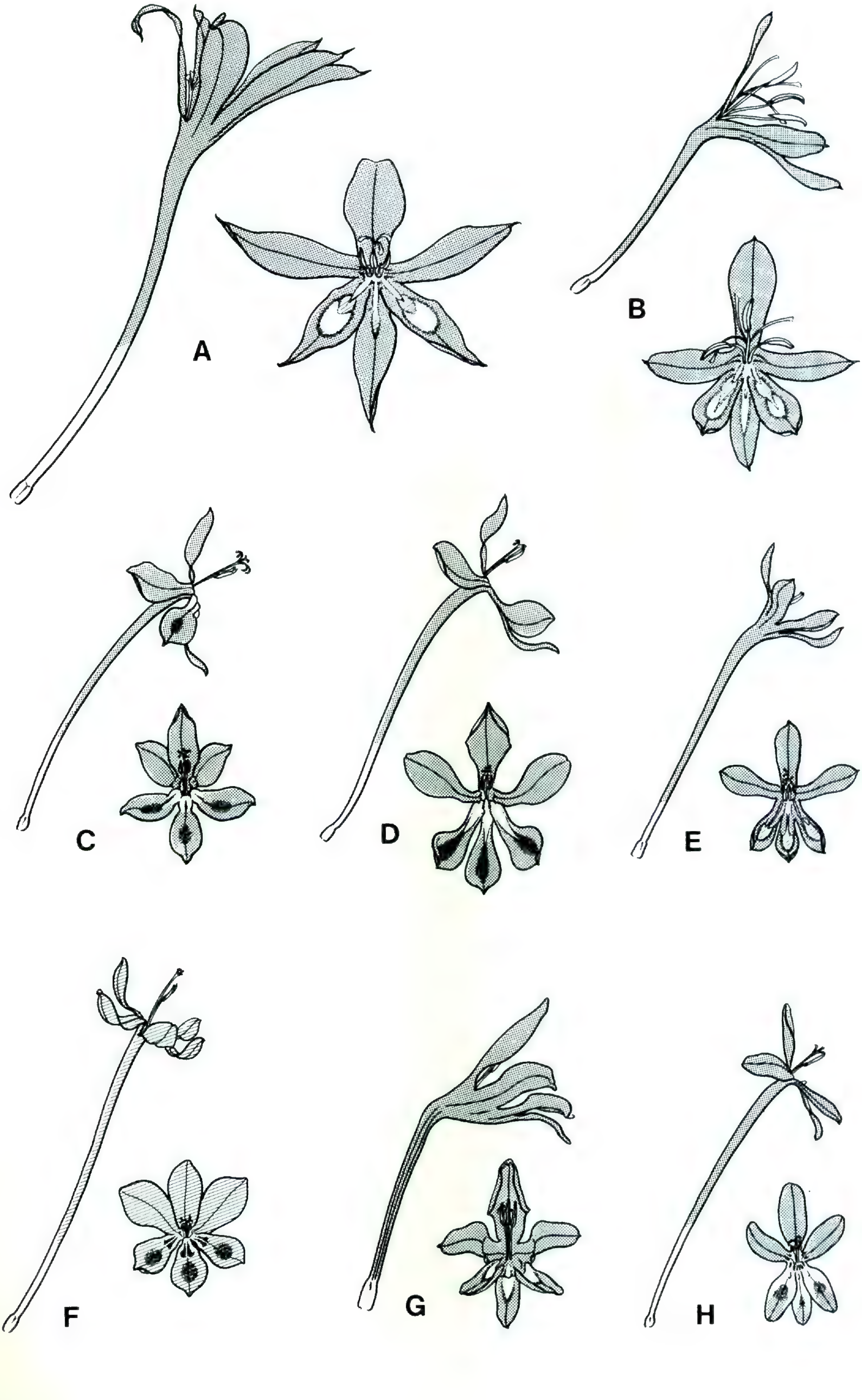
Figure 8. Flowers of species of Iridaceae belonging to the *Lapeirousia silenoides* guild pollinated (or inferred to be pollinated) by *Prosoeca peringueyi.*—A. *Babiana framesii.*—B. *B. curviscapa.*—C. *Lapeirousia pyramidalis* subsp. *regalis.*—D. *L. dolomitica* subsp. *dolomitica.*—E. *L. violacea.*—F. *L. silenoides.*—G. *Sparaxis variegata* subsp. *meteler-kampiae.*—H. *Tritonia marlothii.* (Scale: full size.)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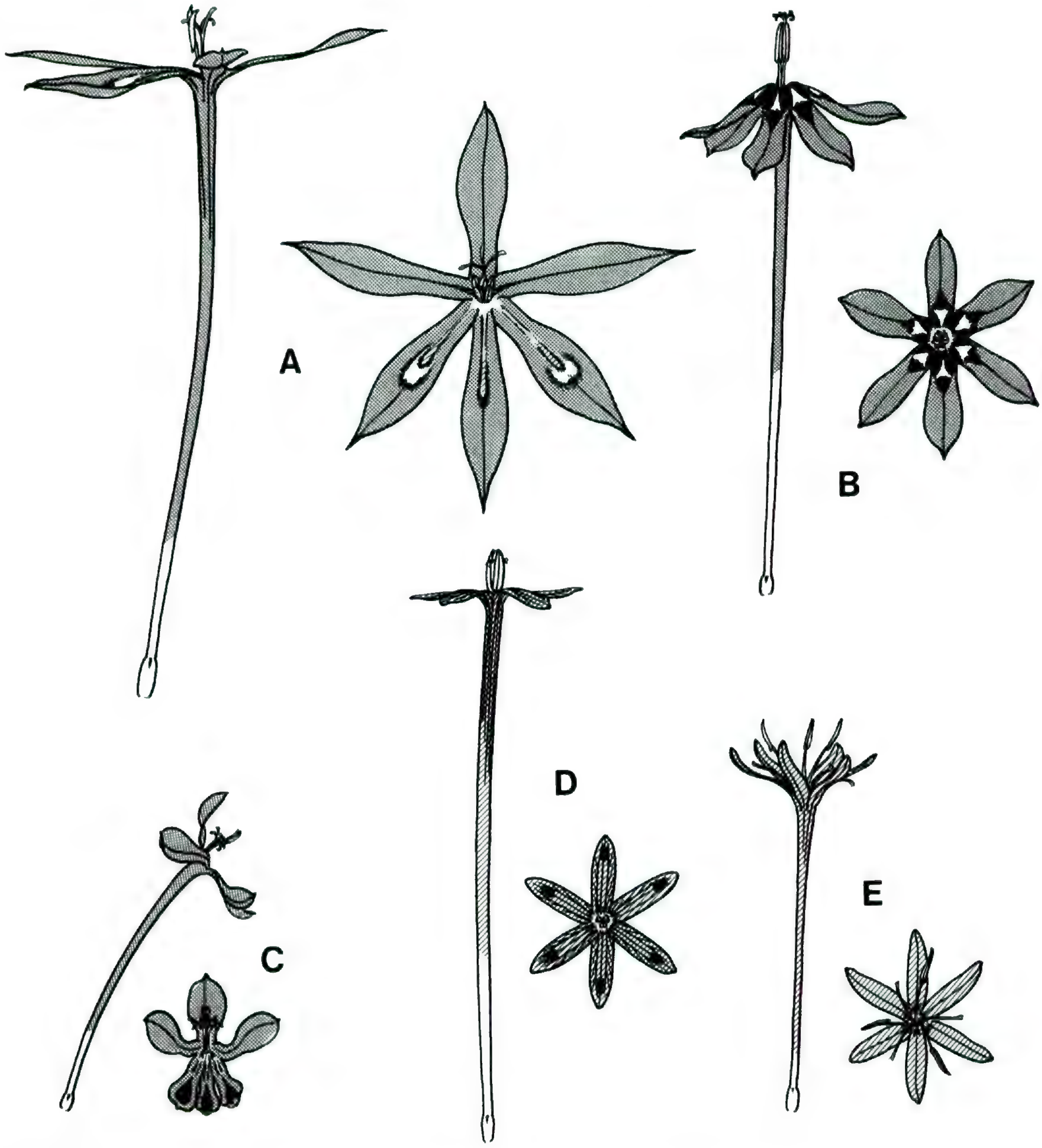

Figure 9. Flowers of species of Iridaceae belonging to the *Lapeirousia silenoides* guild pollinated (or inferred to be pollinated) by *Prosoeca sp. nov.*—A. *Babiana flabellifolia.*—B. *Lapeirousia oreogena.*—C. *L. jacquinii.*—D. *Romulea hantamensis.*—E. *Hesperantha oligantha.* (Scale: full size.)

species of the guild during more than 200 hours of observation time except for three anthophorid bees, which visited but did not forage on individuals of *L. silenoides.* It is almost certain that the plant species for which we do not have pollinator observations will prove to be one or both of these fly species. Because the fly species are allopatric, we have inferred pollinator identity on the basis of the range of the plant species for which we have no observations. *Prosoeca peringueyi* is confirmed as the primary pollinator of three species of Geraniaceae and eleven species of Iridaceae, and *P. sp.* of five species of Iridaceae (Table 4).

GEOGRAPHY

The plant species with the *Lapeirousia silenoides*-type flowers are restricted to coastal and near interior southern Africa, a semiarid region of low, predominantly winter rainfall. The 28 species have a collective range that extends from extreme southwestern Namibia through the western part of North-

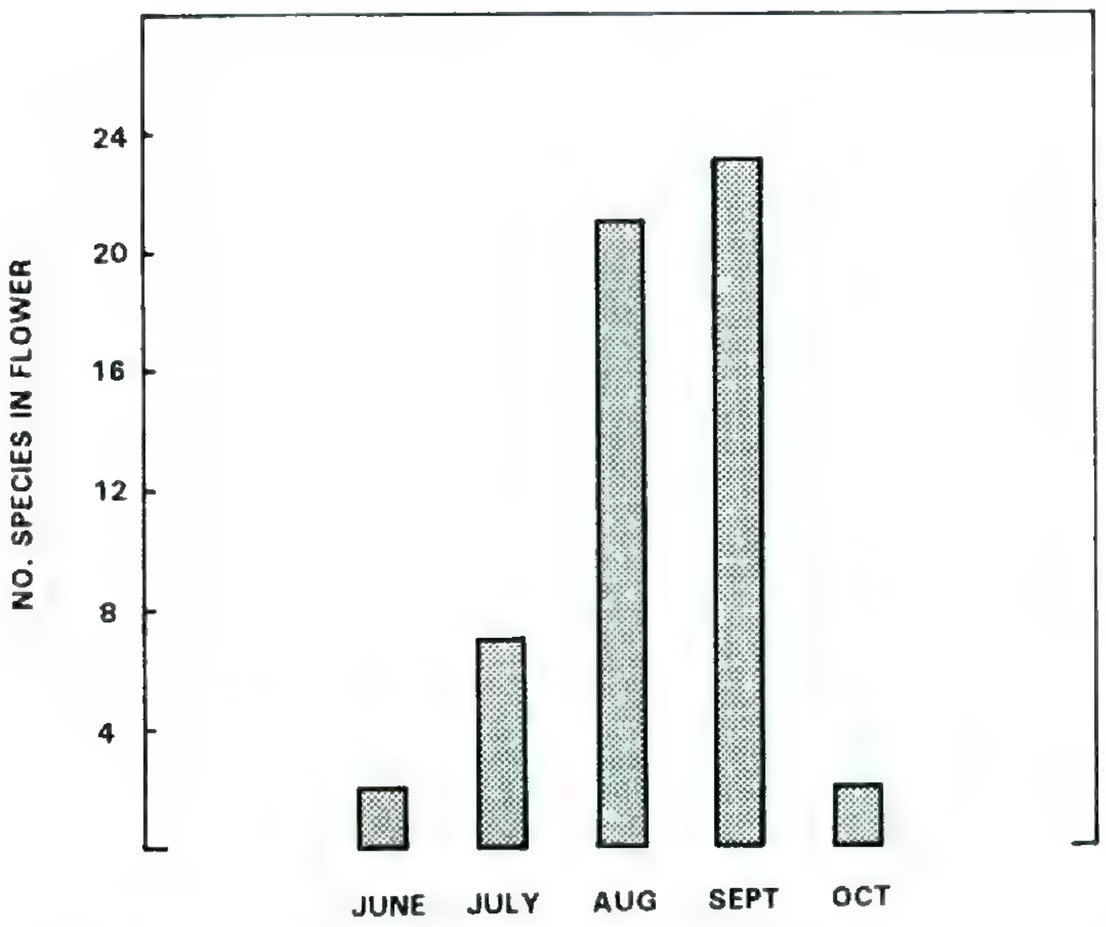

Figure 10. Flowering times of the plant species belonging to the *Lapeirousia silenoides* guild.

ern Cape Province, South Africa, an area known as Namaqualand, and reaches the northwestern portion of Western Cape Province (Fig. 11). The distribution of individual species within this area is often highly local (Goldblatt, 1972, 1984, 1985; Lewis, 1959; van der Walt & Vorster, 1988). At most, seven species of the guild are present in any quarter-degree square, and no more than four guild members co-occur locally. Diversity is greatest in the Kamieskroon area of Namaqualand and in the Pakhuis Mountains of Western Cape Province. Usually the ranges of two or more species overlap. Up to seven species have been recorded in a quarter-degree square of geographical latitude and longitude. Species are infrequent in the north of the range, where only *L. dolomitica* subsp. *dolomitica*, *Tritonia marlothii*, *Pelargonium cortusifolium*, and *P. crassicaule* occur, and along the coast where the putatively autogamous *L. jacquinii* is the only representative.

The combined ranges of *Prosoeca peringueyi* and *P. sp.* (Fig. 12) fall entirely within the main range of the plant species and accord almost exactly with the area within which two or more plant species occur. *Prosoeca peringueyi* has the wider distribution, extending from northern Namaqualand to the Pakhuis Mountains, and *P. sp.* has a localized range along a corridor of high country in Northern Cape Province between Nieuwoudtville and the Hantam Mountains.

POLLEN PLACEMENT

Observation of living and pinned insects, corroborated by pollen washes, confirmed that pollen of a particular plant species is consistently deposited on a limited part of the insect's body (Table 4). We have identified four mutually exclusive sites of deposition: top of the thorax or dorsum; top of the head or frons; the base of the proboscis or face; and underside of the thorax or sternum and abdomen (Fig. 13). *Pelargonium* flowers have declinate stamens so that the filaments and anthers are situated below the mouth of the floral tube (Fig. 7) and pollen deposition is invariably sternotribic. In *P. incrassatum* (Fig. 7C), which has long filaments, pollen is deposited on the underside of the sternum and thorax (Fig. 13D), but in *P. sericifolium* and *P. magenteum* (Fig. 7A, B, 13C), which have very short filaments, deposition is on the face. Species of Iridaceae belonging to the guild have either actinomorphic flowers with symmetrically disposed stamens (Fig. 9B, D, E) or zygomorphic flowers with the stamens unilateral and arcuate (Figs. 8, 9A, C). The anthers are then either held above the mouth of the floral tube or are dorsal to it, and pollen deposition is nototribic (Fig. 13A, B). Filament length is also variable, being short in species of *Lapeirousia* and *Romulea* but relatively long in *Babiana*, and the site of pollen deposition varies accordingly. In species of *Babiana* pollen deposition is mostly on the top of the thorax (in one species on the top and sides), in *Hesperantha* on the ventral head, whereas in *Lapeirousia* and *Romulea* it is on the frons.

Often there are at least two species of the guild, and sometimes more, co-blooming locally and visited indiscriminately by *P. peringueyi*. At such sites, particularly in Namaqualand, *Lapeirousia silenoides*, *Pelargonium incrassatum*, and one species of *Babiana*, either *B. curviscapa*, *B. dregei*, *B. framesii*, or *B. pubescens*, flower together. In the Clanwilliam District *L. jacquinii*, sometimes *L. violacea*, *Pelargonium magenteum*, and a species of *Babiana* and/or *Sparaxis* commonly form part of a local plant community. At sites in the Kamiesberg, central Namaqualand, as many as four co-blooming members of the guild were recorded. *Lapeirousia silenoides*, *B. curviscapa*, *Hesperantha latifolia*, and *Pelargonium incrassatum* were noted near Leliefontein, and on Sneeukop we encountered *Babiana dregei*, *H. latifolia*, and two other presumed members of the guild, *Xenoscapa uliginosa* (endemic there) and *Geissorhiza kamiesbergensis*.

A similar situation prevails with species visited by *Prosoeca sp. nov.* At different sites *Babiana framesii* and either *Lapeirousia oreogena* or *L. jacquinii*, or *L. jacquinii* and *B. sambucina*, or *B. flabellifolia*, *Hesperantha oligantha*, and *Romulea hantamensis* flower concurrently and are visited indiscriminately by the same fly individual. In the above examples, pollen contamination of one spe-

Table 4. Pollinator characteristics and effective tube length of species with the *Lapeirousia silenoides*-type flower. Measurements of insect mouthparts were made from individuals collected on the plant species concerned. Dash in column three reflects no pollinator recorded on that species.

Family/species	Anther to base of tube (mm)	Pollen deposition site	Insect tongue length (mm)
Plants pollinated (or inferred to be pollinated) by *Prosoeca peringueyi*			
Geraniaceae			
Pelargonium			
cortusifolium	ca. 35	ventral head	—
crassicaule	18–35	ventral head	—
echinatum	30–58	ventral head	—
incrassatum	44–52	ventral thorax	28–33
magenteum	37–53	ventral head	30–35
sericifolium	43–66	ventral head	35–40
Iridaceae			
Babiana			
curviscapa	40–55	dorsal thorax	25–28
dregei	47–53	dorsal thorax	25–28
ecklonii	52–65	dorsal thorax	—
framesii	45–50	dorsal thorax	30–35
geniculata	45–55	dorsal thorax	—
pubescens	ca. 62	dorsal thorax	32–35
sambucina			
var. *unguiculata*	38–55	dorsal thorax	—
Geissorhiza			
kamiesmontana	23–32	ventral head	—
Hesperantha			
latifolia	20–35	ventral head	20–25
purpurea	ca. 25	ventral head	—
Lapeirousia			
dolomitica			
subsp. *dolomitica*	25–45	frons	30
subsp. *lewisiana*	40–50	frons	—
jacquinii	35–45	frons	32–35
pyramidalis			
subsp. *regalis*	45–55	frons	32–34
silenoides	45–60	frons	35–40
violacea	40–45	frons	32–35
Sparaxis			
variegata			
subsp. *metelerkampiae*	40–45	frons	32–35
Tritonia			
marlothii	27–46	frons	—
Xenoscapa			
uliginosa	27–32	frons	—
Plants pollinated (or inferred to be pollinated) by *Prosoeca sp nov.*			
Iridaceae			
Babiana			
flabellifolia	50–70	frons	40–45
framesii	45–50	dorsal thorax	40–48
sambucina			
var. *longibracteata*	35–55	dorsal thorax	—
Hesperantha			
oligantha	30–40	ventral head	—
Lapeirousia			
jacquinii	35–45	frons	40–45
oreogena	55–65	ventral head	40–48
Romulea			
hantamensis	60–75	frons	40–45

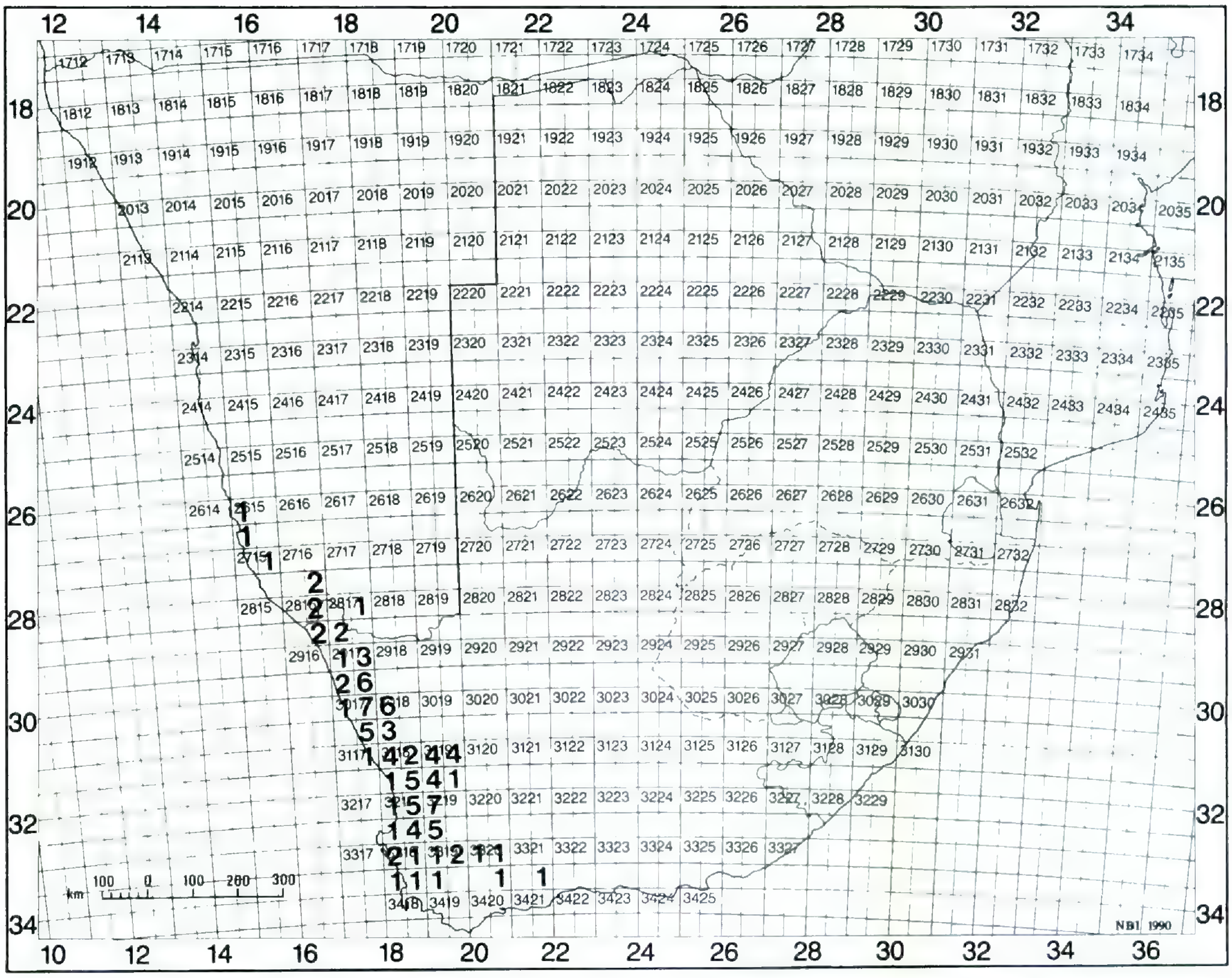

Figure 11. Map of southern Africa showing the distribution range of species with the *Lapeirousia silenoides*-type flower. Figures indicate the total number of species recorded per quarter-degree square of geographical latitude and longitude.

cies by that of another is minimized or prevented by the use of different deposition sites as outlined above. At any study site that included two or more species of the guild, the pollen of each species was placed on a different part of an insect's body (e.g., Fig. 13). The only exception to this pattern was at Botterkloof Pass (and presumably other localities where these two species co-occur) where pollen deposition sites for *Lapeirousia jacquinii* and *L. violacea* are identical.

A crude estimate of potential pollen contamination was determined by comparing the number of guild members recorded from any quarter-degree square with the number of pollen deposition sites utilized by these species. The number of placement positions exploited in any quarter-degree square is positively correlated with the total number of guild members occurring in that grid (Fig. 14). A coefficient of pollen contamination was calculated for grids containing more than one species of the guild by dividing the number of species into the number of loading sites per quarter-degree grid. For the species in the guild the mean coefficient was 0.77, suggesting selection for reduced pollen contamination. The index greatly underestimates the pollen contamination coefficient because not all of the species in a grid co-occur locally. The local co-occurrence of more than one species using the same pollen deposition site is rare, and we only know of the single example mentioned above.

FORAGING PATTERNS

Adult specimens of *Prosoeca peringueyi* have been collected from late July to late September, with a peak during mid August to mid September. Specimens of *P. sp.* have only been recorded from mid August to mid September. Both species have a similar foraging behavior. The flies move rapidly between flowers and hover for two to three seconds while orienting and inserting their proboscis into the floral tube (Goldblatt et al., 1995) (Figs. 3–6). In species with zygomorphic flowers the fly always orients itself in the same way, approaching the flow-

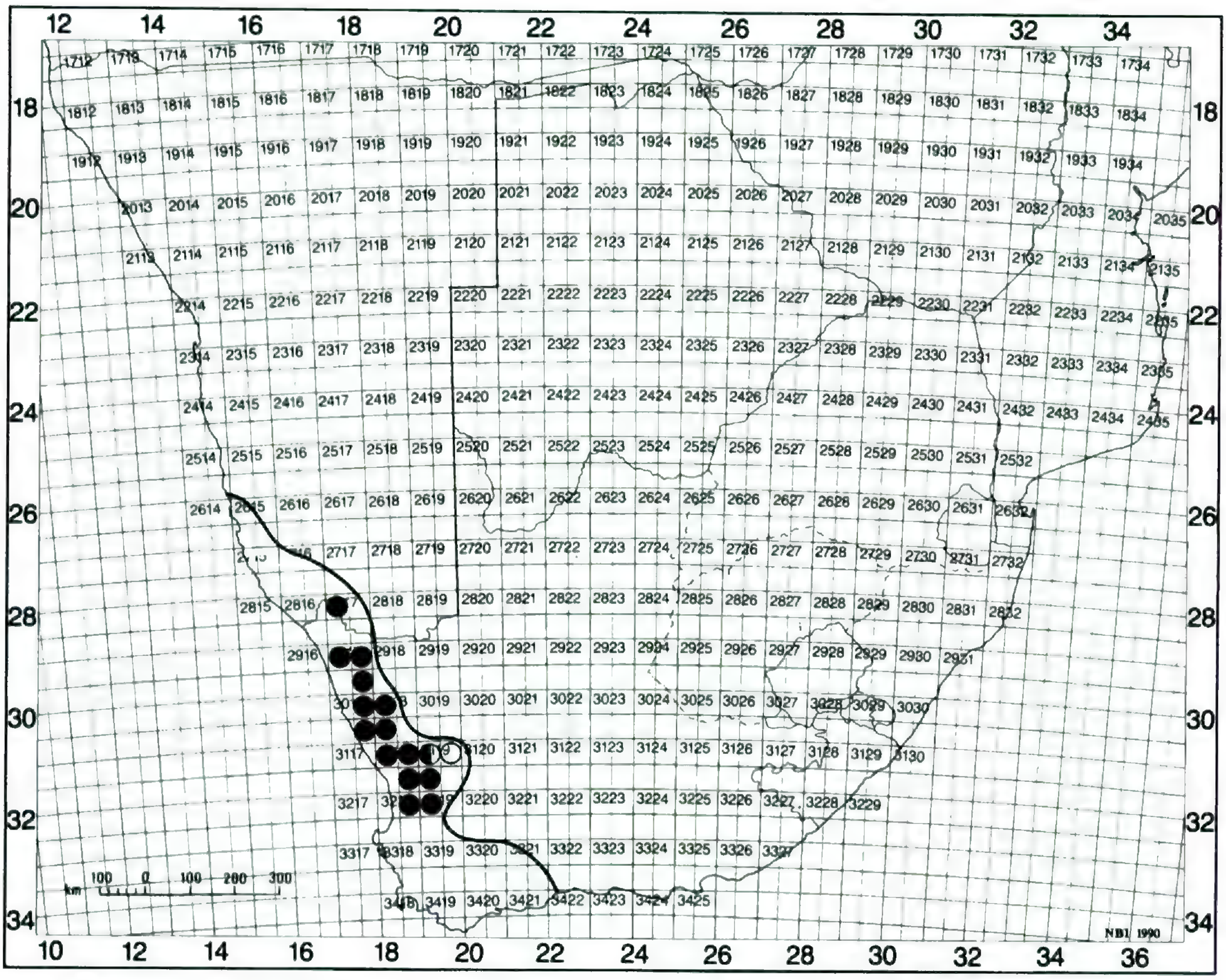

Figure 12. Map of southern Africa showing the distribution ranges of *Prosoeca peringueyi* (closed circles) and *P. sp.* (open circles) recorded on quarter-degree squares of latitude and longitude. The combined ranges of plant species belonging to the guild pollinated by these two fly species is indicated by the heavy outline.

er directly from the front. The flies are unable to discriminate between flowers that have already been visited either by themselves by other individuals and may repeatedly visit the same flower even when all the nectar has been removed (pers. obs.). When nectar is absent visits are brief.

Both fly species are active on mild to warm days from mid morning to early afternoon, and again in the late afternoon. Foraging is most active on warm days between 12:30 and 2:30 PM, but some foraging occurs at almost any time of day. Density of visitors varies considerably, ranging from 4 to 5 flies present locally at the same time, or as few as 1 or 2 over periods as long as an hour. Flies remain at each flower for 3–5 seconds, and pollen is passively brushed onto various parts of the head, thorax, or abdomen, depending on the species visited. Pollen depositions are usually heavy enough to be visible to the naked eye against the dark bodies of the insects. Commonly, pollen of two or three different species can be distinguished by color, that of each species located on a different part of the body.

Discussion

The *Lapeirousia silenoides*-type floral syndrome

Our observations indicate that plants with flowers conforming to the following syndrome constitute a guild adapted for pollination by the long-proboscid flies, *Prosoeca peringueyi* and *P. sp. nov.*: perianth or hypanthium tube narrow, straight or slightly curved, and 30–60 mm long; tepals or petals short in relation to tube length and pigmented dark purple to crimson, or sometimes lilac or pale mauve, with nectar guides consisting of white to cream spots and streaks and areas of darker pigmentation; and exserted and prominent anthers and stigmas that are presented outside the mouth of the tube so that they will contact the body of any animal that probes the floral tube. Associated with these features is the production of nectar with a relatively

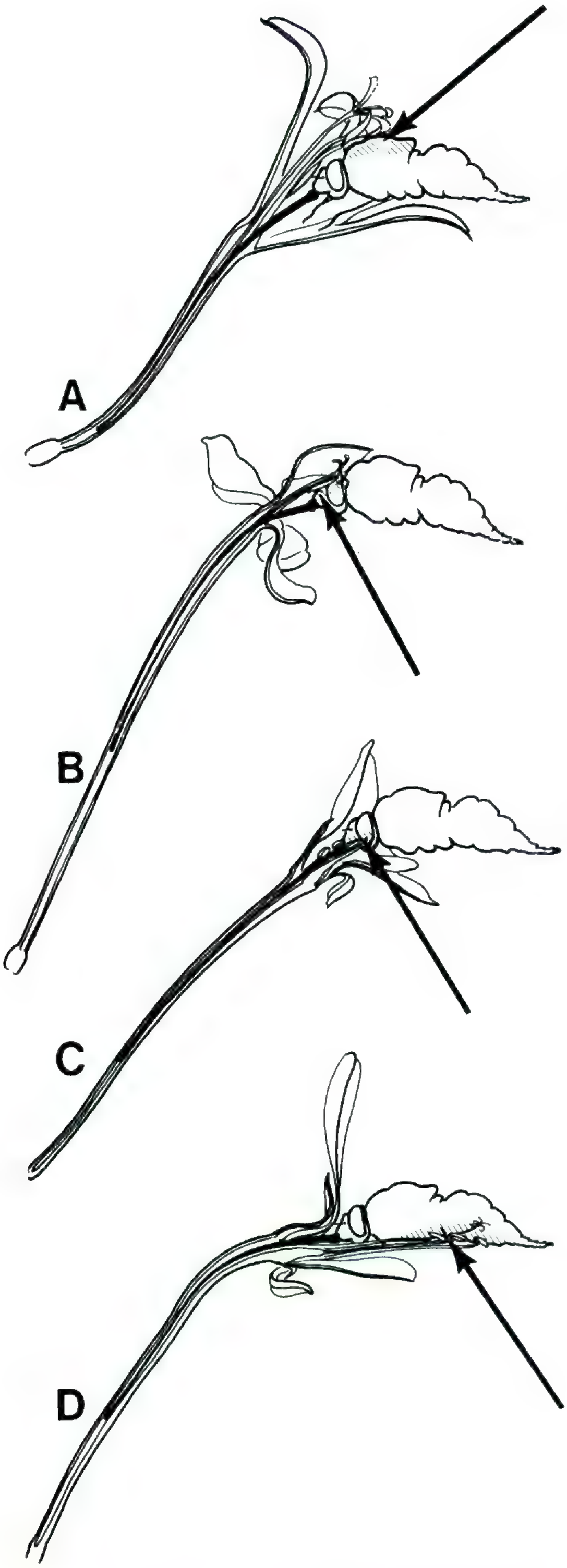

Figure 13. Differential placement of pollen on *Prosoeca peringueyi*.—A. *Babiana curviscapa*, dorsum.—B. *Lapeirousia silenoides*, frons.—C. *Pelargonium sericifolium*, face.—D. *P. incrassatum*, sternum (ventral thorax and abdomen). Hatching indicates the site of pollen deposition. (Scale: full size.)

high sugar concentration and the absence of floral odor (present in two species). The plant taxa occurring north of 29°S, i.e., in the Richtersveld and southern Namibia, comprise a distinct subset of the guild characterized by the paler-colored lilac or pale mauve flowers. This group comprises *Lapeirousia dolomitica* subsp. *dolomitica*, *Tritonia marlothii*, *Pelargonium cortusifolium*, and *P. crassicaule*.

Only *Pelargonium sericifolium* has no measurable floral nectar; we presume that it is an example of pollination by deceit (Goldblatt et al., 1995). In color and shape the flowers closely resemble those of *Lapeirousia silenoides* and *P. magenteum*. These species frequently co-occur with *P. sericifolium* and have ample amounts of nectar of relatively high sugar concentration. Two species of *Babiana* and one subspecies of *L. dolomitica* are exceptional here in having sweetly scented flowers. Presence of scent is usually considered to add to the attractiveness of the flowers, but in *Babiana* we are inclined to consider it a vestigial trait in view of its rarity among members of the guild. Most of the species of *Babiana* sect. *Babiana*, to which the *Prosoeca*-pollinated species belong, have strongly scented flowers and are bee pollinated (e.g., *B. odorata*, *B. scabrifolia*, unpublished observations).

Nectars of moderate sugar concentration and typically sucrose-rich to sucrose-dominant seem to be characteristic of plants pollinated by active insects such as bees of the family Anthophoridae and by long-tongued flies (Goldblatt et al., 1995), although not of plants pollinated by other Diptera (Baker & Baker, 1983, 1990) such as Calliphoridae, Muscidae, and Tachinidae. The nectar sugar concentrations of flowers pollinated by *Prosoeca* and other Nemestrinidae (Table 2) are typically somewhat lower than those of bee-pollinated flowers. This may be related to the difficulty of sucking up liquids of higher viscosity, as is the case in long-tongued butterflies (Johnson & Bond, 1994). The low sucrose to hexose ratios in the two species of *Pelargonium* (Table 2) contrast with the pattern in Iridaceae belonging to the guild. Species of *Pelargonium* are visited as avidly as any of the Iridaceae. Indeed, on the basis of the frequency of visits, *Pelargonium incrassatum* appears to be one of the most important nectar sources for *P. peringueyi*. This leads us to conclude that nectar sugar composition is not a significant factor in the *P. peringueyi* pollination guild.

Not all species with long perianth tubes and dark purple to crimson flowers belong to the guild. In some species that have flowers apparently conforming to the guild the lower part of the perianth tube

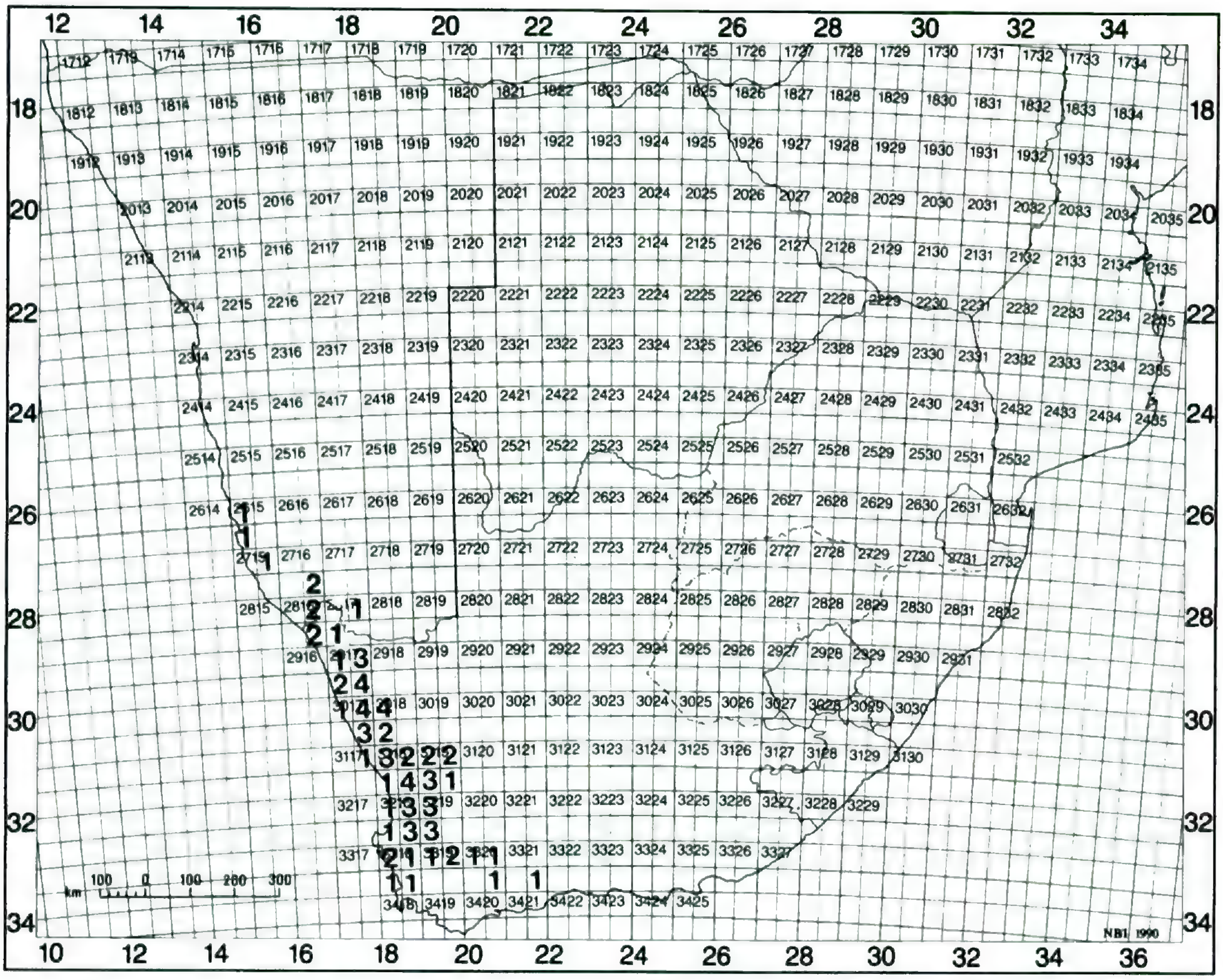

Figure 14. Map of southern Africa showing the differentiation of pollen loading sites. Figures indicate the number of different pollen-loading sites utilized by plant species per quarter-degree square of geographical latitude and longitude. The total number of species occurring in each grid is indicated in Figure 11.

is so narrow as to effectively prevent the penetration of an insect's tongue. In these cases nectar is forced into the upper part of the tube where it is accessible to a variety of insects. Long-tongued flies visiting these species may obtain nectar but will not come into contact with the pollen and stigmatic surfaces. This situation has already been described for the long-tubed species *Lapeirousia montana*, which superficially appears to be a member of a long-tongued insect pollination guild (Goldblatt et al., 1995). The tube is up to 43–55 mm long, but is so narrow in the lower half that the nectar is forced upward and lies only 10–15 mm from the mouth of the tube. The flowers are visited by a variety of bees, Lepidoptera, and bombyliid flies, all of which may accomplish pollen transfer. Likewise, we have found that whereas *B. sambucina* var. *longibracteata* and variety *unguiculata* do conform to the guild except in their scented flowers, variety *sambucina* does not. Although the perianth tubes of all three varieties are 30–55 mm long, in variety *sambucina* the lower part of the tube is effectively blocked and nectar is forced into the top of the cylindrical part of the tube where it is accessible to a variety of insects. The situation in variety *sambucina* is no surprise because its distribution range is mostly outside that of *Prosoeca peringueyi* or *P. sp.* A comparable situation exists in *Babiana dregei*, which has a tube 50–65 mm long, thus longer than the mouthparts of *P. peringueyi*. In this plant, too, the tube is narrowed in the lower 20–30 mm rendering the functional tube length much shorter than the external length, and the nectar is thus available to individuals of *P. peringueyi* with tongues of moderate length.

Color of the perianth and of the nectar guides may also be misleading. *Babiana pauciflora* G. Lewis has purple flowers with tubes 35–45 mm long, but a strong fragrance, bright yellow nectar guides, and a flowering period of June appear to exclude the species from the guild. *Babiana attenuata* G. Lewis and *B. truncata* G. Lewis also have

perianth tubes in the 30–45-mm-long range, but the blue or mauve flowers have yellow nectar guides and, in the case of *B. attenuata*, fragrant flowers. We do not regard them as guild members.

THE *PROSOECA PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi–P. sp.* pollination guild (hereafter referred to simply as the *P. peringueyi* pollination guild) is unique in its combination of a long floral tube with a distinctive perianth coloring, and its restricted occurrence in so small a part of southern Africa is striking. While a long-tongued fly pollination syndrome has been described for the Cape Flora (Whitehead et al., 1987), this covered only plants with cream to pink flowers with dark nectar guides. The *P. peringueyi* guild thus deviates significantly from other long-tongued fly pollination systems. There are at least two other guilds of plant species adapted for long-tongued fly pollination in southern Africa. Late spring- and early summer-flowering species with white to cream flowers with red nectar guides (e.g., *Lapeirousia anceps* (L.f.) Ker-Gawl., *L. fabricii* (Delaroche) Ker-Gawl.) are pollinated by either *Moegistorhynchus longirostris* (Nemestrinidae), or *Philoliche gulosa*, or *P. rostrata* (Tabanidae) (Vogel, 1954; Goldblatt et al., 1995). Summer- and autumn-flowering species with long-tubed, blue, pink, or white flowers (e.g., *Nivenia stenosiphon* Goldblatt (Iridaceae, Goldblatt & Bernhardt, 1990), *Disa oreophila* H. Bol. (Orchidaceae, pers. obs.), *Gladiolus microcarpus* G. Lewis (Iridaceae, pers. obs.), and *Zaluzianskya microsiphon* (O. Kuntze) K. Schum. (Scrophulariaceae, pers. obs.)) are pollinated by *Prosoeca ganglbaueri* over a wide portion of southern Africa. Both these syndromes are quite distinct from the *Prosoeca peringueyi* pollination system in the flower color, plant and insect distribution, pollinator identity, and flowering time.

Tongue length is surprisingly variable in *Prosoeca peringueyi* and somewhat variable in *P. sp.* The variation corresponds locally to floral tube length of their nectar plants. In the Kamiesberg Mountains where *Hesperantha latifolia*, *Babiana dregei*, and *Pelargonium incrassatum* are major nectar sources and effective tube length is 20–40 mm, *P. peringueyi* has a tongue of 20–25 mm long. In other places in Namaqualand where *L. silenoides* and *B. pubescens* have floral tubes in excess of 50 mm, individuals of *P. peringueyi* have tongues 35–40 mm long. In the Olifants River Valley where *L. pyramidalis* and *L. jacquinii* are major nectar sources for *P. peringueyi* and have tubes 35–45 mm long, flies caught on these species have tongues 30–33 mm long. Clearly local variation in tube length in the flowers of food plants is tracked by the pollinator.

The disparity between the length of floral tube in plants with the *Lapeirousia silenoides*-type flower and the shorter length of the mouthparts of the sole pollinators is quite easy to explain (Goldblatt et al., 1995). Records of nectar secretion show that these flowers secrete ample amounts of fluid for insect-pollinated flowers, and it is unlikely that dominant pollinators are ever forced to extend their mouthparts to the base of the tube unless all the nectar has been removed by earlier foragers. More importantly, Darwin (1877) hypothesized that successful pollination of spurred orchids occurred when orchids evolved floral spurs slightly longer than the tongues of their pollinators, ensuring maximum contact between the insect's head and the orchid's column by forcing the insect to ram its head down the floral throat. This has since been shown experimentally by Nilsson (1988). As in the nectariferous orchids, species with the *L. silenoides*-type flower force their pollinators to make maximum contact with the anthers and stigmatic surfaces that block or at least encircle the entrance to the floral tube.

The combined geographical ranges of all the species pollinated primarily by *Prosoeca peringueyi* and *P. sp.* (Fig. 11) are greater than the ranges so far recorded for the two fly species (Fig. 12). To the north in southern Namibia *P. peringueyi* may simply not have been collected yet. To the south, essentially below the 33rd parallel and west of the 19th north-south parallel, the guild is represented mainly by *L. jacquinii*. This species is known to be autogamous (Goldblatt et al., 1995), although it is actively pollinated by both species of *Prosoeca* within their ranges. Presumably autogamy has enabled it to extend its range outside that of its facultative pollinators. The only other species that occurs outside the ranges of the two flies is *Pelargonium magenteum*. The reasons for its wider distribution to the east of the range of *P. peringueyi* and *P. sp.* are unknown.

The potential for pollen contamination from other members of the same guild is greatly increased for plant species that share a single specialized pollinator species. One strategy to enhance segregated gene flow is differential placement of pollen on the insect body. This strategy is developed in Orchidaceae (Dressler, 1968a, b; Manning & Linder, 1992), Scrophulariaceae (Steiner & Whitehead, 1988, 1990), and various other families (Grant, 1994). In flowers of species belonging to the *P. peringueyi* pollination guild, four mutually exclusive sites have been identified. In this guild the contamination coefficient is never below 0.5, suggesting

that there is a threshold of pollination efficiency that determines the number of species that can effectively use the same loading site. In view of mechanical constraints on flower architecture in the genera involved, there appears to be a definite limit to the number of species that can enter the guild at any locality. Pollination contamination may thus be a significant factor in influencing species packing in specialist systems. Locally, the niche offered by pollination by *Prosoeca peringueyi* or *P. sp.* appears to become saturated by the presence of more than three co-flowering species. The presence of four similarly adapted species is rare.

Differential placement of pollen on an insect's body demands precise orientation of the pollinator relative to anther position. Floral zygomorphy facilitates this, and we suggest that this is an important factor in favoring genera with predominantly zygomorphic flowers.

The *Lapeirousia silenoides* pollination syndrome appears to have evolved in five different lineages in *Lapeirousia* subg. *Lapeirousia*, a taxon that includes just 21 species (Goldblatt et al., 1995). A comparably polyphyletic evolution of the syndrome appears to have occurred in *Babiana* and in *Pelargonium*, as species with this syndrome in these genera are taxonomically isolated.

ORIGIN OF THE *PROSOECA PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi* pollination guild involves at least six genera of plants in two families and two species of *Prosoeca* (Nemestrinidae). Although the plant species belonging to the guild and their pollinators are restricted to western southern Africa, all of the genera, both plant and insect, extend beyond the range of the guild. Other species of *Prosoeca*, both long- and short-tongued, visit flowers of various colors including white, cream, pink, lilac, blue, and yellow (Johnson, 1992; Goldblatt et al., 1995; pers. obs.). *Prosoeca peringueyi* has been observed visiting species outside the guild for nectar that are pale lilac or pink and green in color. In addition, the northern taxa of the guild are lilac or pale mauve and some have been confirmed to be pollinated by *Prosoeca peringueyi*. The original determinant for the characteristic crimson or purple color in the guild was thus apparently not directed by the innate preference of *P. peringueyi* for that particular flower color, and was in consequence presumably plant-directed.

Comparative studies of each of the guild genera suggests that pollination by long-tongued flies is apomorphic. Of the guild members only *Babiana* has flowers in which dark blue or violet color is the plesiomorphic condition. In addition, even short-tubed species of this genus secrete fairly large amounts of nectar. Also, *Babiana* has flowers with a wide gullet, which makes access to the pollinator mouthparts easier than the narrow-tubed flowers in the other guild genera, for example, *Lapeirousia* and *Pelargonium*. These factors suggest to us that the first steps in the development of the *Prosoeca peringueyi* pollination system were through the genus *Babiana*. Significantly, both *Babiana* and *Lapeirousia*, the two genera that individually have the most species in the guild and together comprise 54% of the guild, are largely developed in arid habitats. It may be that the origin of the syndrome in *Babiana* and its subsequent development in species of *Lapeirousia* was a consequence of higher species richness in these genera in the western part of southern Africa. The predominant dark purple flower color in *Babiana* would explain the characteristic floral coloring in the *L. silenoides* pollination syndrome, unknown in other *Prosoeca* pollination guilds. Subsequently, species in other genera could be expected to enter the guild in response to the reproductive benefits derived from these pollinators.

The advantages to the plant species of a dedicated pollinator are obvious and include increased pollination success and decreased pollen contamination and loss. Pollination success in one population of *Lapeirousia pyramidalis* subsp. *regalis* that we investigated was 45% (SD ± 25%; n = 23). To the pollinator, however, the energetic rewards of floral specialization are important. For large active insects that hover while foraging the energy demands are likely to be high. Long-tongued nemestrinids are capable of feeding from short-tubed flowers, but these are smaller and hold far less nectar than that typically present in the long-tubed flowers in the guild. In addition, the flies are in competition with other insects that can obtain the nectar in short-tubed flowers. Long-tubed flowers can contain large amounts of nectar that cannot be collected by short-tongued insects. They are therefore an attractive energy source for insects able to exploit it.

We speculate that there is reduced pressure to darken the flower color in the northern members of the guild. This more arid region supports both fewer plants and fewer pollinators, and a more facultatively generalist pollination system might be favored. This is borne out by the greatly extended flowering periods of *Pelargonium cortusifolium* and *P. crassicaule*, which although peaking in August and September are prolonged far beyond the flight period of *Prosoeca peringueyi*. During this time they

are presumably visited by other insects, perhaps bees and bee flies. Significantly, both species have short anthers, which will contact visitors of a range of shapes and sizes. Possibly a threshold diversity is necessary before selection pressures become strong enough to favor such specialist pollination systems.

EVOLUTIONARY IMPLICATIONS OF THE *PROSOECA PERINGUEYI* POLLINATION GUILD

The *Prosoeca peringueyi* pollination guild appears as distinct as other highly specific pollination systems in the African subcontinent, including those involving sunbirds, *Nectarinia* species (Rebelo, 1987), oil-collecting bees in the family Melittidae (Steiner & Whitehead, 1990, 1991a), resin-collecting bees in the family Megachilidae (Steiner & Whitehead, 1991b; Armbruster & Steiner, 1992), other guilds of long-tongued flies (Goldblatt et al., 1995; Johnson & Steiner, 1995; Manning & Goldblatt, 1995), and the butterfly, *Aeropetes tulbaghia* (Johnson & Bond, 1994). Where such systems occur they contribute to the particular floral characteristics of various plant communities.

The recognition of the *Prosoeca peringueyi* pollination syndrome and the way it functions is the key to understanding the presence of a series of species with unusual dark purple or crimson flowers with long floral tubes in the flora of coastal and near interior western southern Africa. The ecological niche presented by these two flies is so specific that it will allow fly-pollinated and non-fly-pollinated members of the same genus flowering at more or less the same time to coexist with little or no hybridization. The diversity of pollination systems there is one of the reasons why some 30 species of *Babiana* (50% of the total species) and 19 species of *Lapeirousia* (48% of the total) co-occur in this area.

Like the members of the *Aeropetes tulbaghia* pollination guild (Johnson & Bond, 1994), there is strong similarity in floral morphology between members of the *Prosoeca peringueyi* guild. This suggests strong selection for floral conformity. This may be a characteristic of guilds in which the pollinator is an insect that is not flower constant.

Prosoeca peringueyi and *P. sp. nov.* may be regarded as keystone species. Such species are defined operationally as those that, by their effective disappearance from a system, would cause (directly or indirectly) the virtual disappearance of several other species. The extinction of either *P. peringueyi* or *P. sp. nov.*, but especially the former, would result in significant decreases in seed set in many of the species in the *P. peringueyi* guild, prevent outcrossing, and might lead to their ultimate extinction.

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REVISION OF *PAVETTA* SUBGENUS *BACONIA* (RUBIACEAE: IXOROIDEAE) IN CAMEROON[1]

Stephen D. Manning[2]

ABSTRACT

Pavetta subg. *Baconia* (Rubiaceae tribe Pavetteae) is a group of forest shrubs in tropical and subtropical Africa. It includes species of *Pavetta* with bearded corolla throats, corolla tubes usually shorter than corolla lobes, terete or subterete style tips, and fruits usually of colors other than black. Cameroon is a major center of diversity for subgenus *Baconia*, and the Cameroon species are revised here. Twenty-nine species are recognized, including eleven newly described; five previously recognized species are placed in synonymy. Seven series used earlier to subdivide subgenus *Baconia* have been abandoned owing to inconstancy of character states used to delimit most of them. Sixteen Cameroon species are presently unreported from elsewhere. Infraspecific taxa are recognized in seven of the twenty-nine species. Aspects of leaf morphology are useful taxonomically. An overview is provided of these, other aspects of morphology, habitat preferences, and reproductive strategies. Habitat preferences, distributions, and distinguishing features follow descriptions of each species.

Pavetta L. consists of about 400 species of shrubs (less often small trees or geofrutices) in forest understories (less often savannas) of the paleotropics and paleosubtropics. Its center of diversity is in Africa. Most taxa bear characteristic bacterial nodules sensu Lersten & Horner (1976) on their leaves (Zimmermann, 1902; von Faber, 1912; Lersten, 1974, 1975; Lersten & Horner, 1976). Most species are infrequently collected. The similar genus *Ixora* L. is distinguished from *Pavetta* in having style tips recurved at maturity, and no species of *Ixora* have bacterial nodules (Bremekamp, 1934). The taxonomic history of *Pavetta* is recounted by Bremekamp (1934: 12–13), who produced the only comprehensive monograph of the genus (1934, 1939a, 1939b). By 1939 Bremekamp had recognized 377 species, 206 described by himself, and 3 subgenera: *Eupavetta* Bremek., correctly referred to as subgenus *Pavetta* (316 species, Africa, Arabia, Asia, tropical Australia, Sri Lanka, Melanesia, Philippines); *Baconia* Bremek. (58 species, all African); and *Dizygoön* Bremek. (3 species, all tropical African).

De Candolle (1807) described the monotypic genus *Baconia* DC. with *B. corymbosa* DC. (presently *Pavetta corymbosa* (DC.) F. N. Williams). He distinguished *Baconia* by its 4-merous flowers not surrounded by bracts, bearded corolla throat, nonciliated stipules, projecting anthers, and "simple stigmas." *Baconia* was reduced to synonymy of *Pavetta* by Bentham and Hooker (1873), followed by Hiern (1877). Bremekamp (1934) recognized *Baconia* as a subgenus, including members of *Pavetta* with the following characters: bearded corolla throat; short, stout corolla tubes; minute bracteoles at flower bases; and white or colored drupaceous fruits. This group was kept by Bremekamp within *Pavetta*, rather than restoring it as a genus, because of its tetramerous flowers, cylindrical upper part of style, small stigmatic lobes, and, in most species,

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bacterial nodules. Since then, new taxa have been described and others placed in synonymy within subgenus *Baconia* (e.g., Bremekamp, 1953, 1956; Adam, 1973; Bridson, 1978), but its circumscription remains otherwise unchanged. The defining character is the bearded corolla throat; other characters listed by A. P. de Candolle, Bremekamp, and others are not universal or are shared with related taxa.

Bremekamp (1934: 21) noted that the species of subgenus *Baconia* were closely related and did not divide it into sections as he did subgenus *Pavetta*. He divided it into seven series based on number of ovules per locule and branching, nodule, and vestiture characters. Added collections since then reveal that, within series (even within species), characters upon which series were separated are not constant. Those series are thus not recognized here. Similarly, Bridson (1978) and Bridson and Verdcourt (1988) did not recognize the series in treatments of East African species.

Methods

Classical alpha taxonomy methods were used in this study, supplemented by field observations and collections in Cameroon. In addition, certain characters (whether more than 10% of calyx lobes overlap at the base at maturity, whether the corolla throat beard characteristic of subgenus *Baconia* extends onto the corolla lobes, calyx lobe shape and length, corolla lobe and tube lengths, style exsertion length, leaf venation pattern, and leaf venation density) were treated morphometrically. Their averages sometimes distinguish species despite overlapping intraspecific ranges. At least 10 and, when sufficient material was available, 20 or more measurements per taxon were made for such characters to determine the average character state. Chi-square analyses were performed to determine whether taxa had more than 10% of their calyx lobes overlapping at the base at the $p = .05$ confidence level.

Habit

All of the 29 species of *Pavetta* subg. *Baconia* in Cameroon are woody. The majority are understory forest shrubs 1–5 m tall when flowering or fruiting. Representatives of seven species have been recorded on herbarium labels as taller than 5 m.

Vestiture

Vestiture, when present, consists of unbranched erect to appressed or less often reflexed trichomes from less than 0.01 to more than 0.5 mm long; trichomes toward the short end of this range are more common than longer ones.

Stems

The main stems of *Pavetta* subg. *Baconia* are monopodial, usually with limited branching. Branches are usually monopodial but occasionally exhibit sympodial growth, e.g., in *P. baconiella* Bremekamp. The branches are often floriferous twiglets with terminal inflorescences. Limited vegetative lateral branching also occurs. Vestiture ranges from absent to dense, the density often increasing toward the apex.

Leaves

As in nearly all Rubiaceae, leaves are simple and opposite with margins entire, although a slightly undulate margin sometimes occurs. Leaves are almost always darker green above than below. Leaves vary from membranaceous to coriaceous and are usually chartaceous to subcoriaceous.

Anisophylly. In most species, pairs of leaves immediately or one node below inflorescences are sometimes unequal in size; the degree of anisophylly varies within species. Anisophylly is never present at all nodes. Leaf blade size ranges described include anisophyllous leaf pairs.

Blade size and shape. Leaf blade size and shape are variable within species and overlap between species. Used with caution, these are nevertheless useful and convenient taxonomic characters in some species. See Manning (1991) for estimates of reliability of leaf size and other characters in *Pavetta rigida* Hiern (subg. *Pavetta*).

Acumens. Most species have leaves with tapering acumens, but some leaves lack acumens in most species. Typical acumens in subgenus *Baconia* are about 10 mm long and 5 mm across at the base.

Apices. Descriptions of apices here include those of nonacuminate leaves and of acuminate leaves below their acumens, as if the directions of the two converging leaf margins below the acumen continued unchanged until they met. In most species, most leaf apices are acute and some are obtuse.

Bases. In all species leaf blade bases are at least occasionally attenuate part or all the way to their point of attachment to the stem as seen at 10×. To the naked eye, most bases appear cuneate or subcuneate, some appear attenuate, and there is significant variation within most species. Asymmetrical bases are common in subgenus *Baconia*.

Venation patterns. Venation characters are described in some detail below and included in species descriptions because they are of diagnostic value, have not been emphasized previously, and are used in keys. They are reported as visible on illuminated, untreated leaves at 10× magnification. Terminology and definitions follow Hickey (1973) except measures of venation prominence and density, described below.

Leaves in subgenus *Baconia* have brochidodromous to eucamptodromous venation. Intermediates are very common, i.e., secondary veins usually branch and become smaller near leaf blade margins but these branches then join the next most distal secondary vein near the leaf margin.

Whether leaf venation, especially fourth- and fifth-order veins, is more easily visible above, below, or neither when illuminated at 10× is usually characteristic of species and thus of taxonomic value at the species level.

Venation prominence. Venation is classified here as prominent, prominulous, intermediate, obscure, impressed, or invisible. Prominent and prominulous veins occur only on lower leaf surfaces. Prominent venation is a term reserved for leaves in which veins protrude from leaf blades most conspicuously to the naked eye. Prominulous means subprominent, though prominulous veins do clearly and significantly protrude below the leaf blade. Vertical protrusion of more than 0.5 mm may qualify a vein to be prominulous; often at least 180° of arc of the vein is visible. Obscure means hard to see when illuminated at 10×. Impressed venation means veins are at a lower level, as seen from above, than the upper leaf surface. The upper leaf surface usually arcs downward toward the veins and upward between them. Venation is intermediate in prominence if not described as prominent, prominulous, obscure, impressed, or invisible.

Prominulous leaf veins are very common. On individual leaves, veins often grade from prominulous near the base to intermediate near the apex.

Tertiary veins. Tertiary veins vary from sometimes orthogonal reticulate through random reticulate to most commonly percurrent, i.e., "tertiaries from the opposite secondaries joining," sensu Hickey (1973), though they sometimes branch. Tertiary veins are usually oblique to the midrib, but occasionally subperpendicular to it.

Higher order veins. Fourth- or fifth-order veins are reticulate. With rare exceptions, the areoles sensu Hickey (1973) so formed range from 0.2 to 3 mm across; the majority are 0.5 to 2 mm across. Veins forming areoles further branch into veinlets terminating inside areoles with or without yet further branching. Areolation in most species is imperfect sensu Hickey (1973), i.e., forming "meshes of irregular shape, more or less variable in size."

Venation density. Leaf venation density was determined by counting the number of veins or veinlets crossed per millimeter of straight line distance on blades, then averaging at least 10 such counts per taxon counted. Veins or veinlets crossed include any veins from secondaries to the lowest order veinlets seen on herbarium specimens illuminated at 10×. Including the midrib or areas very close to margins was avoided when possible. Otherwise measurement locations were selected subrandomly except (1) when only small portions of leaf surfaces revealed higher order venation clearly, such portions were used and (2) measurements were intentionally spread over different specimens when more than one specimen was available.

Density data in species descriptions are all based on averages of counts performed as above and range from two veins or veinlets crossed per millimeter in *Pavetta grossissima* S. D. Manning (very coarse) through three (coarse), four (medium), five (fine), six (very fine), to seven per millimeter (extremely fine) in *P. tenuissima* S. D. Manning. Density is most often medium to fine. This character is of diagnostic value in species having unusually coarse or fine leaf venation. Single density measurements are occasionally significantly higher or lower than average for a taxon, so at least several counts must be made on each plant for which this character is used diagnostically.

Domatia. Along veins on lower leaf surfaces of most species are hollows, areas of denser vestiture than the rest of the leaf, or both. These occur most often in angles of branch veins along midribs, sometimes along secondaries, and occasionally along tertiaries. The descriptions of these structures here as tuft, pocket, pit, crypt, and intermediate between pit and crypt are sensu Robbrecht (1988).

Although some taxa are relatively constant with respect to presence and types of domatia, others are quite variable. Even in species that usually bear domatia, not every branch vein angle along the midrib has a domatium, and whole leaves or specimens may lack domatia.

Nodules. In leaves of over 80% of *Pavetta* species, including African and other species of subgenus *Pavetta* and a similar percentage of subgenus *Baconia*, are black growths termed bacterial nodules (Bremekamp, 1934; Lersten, 1974, 1975; Lersten & Horner, 1976) or leaf galls (Robbrecht, 1988, including illustrations). These vary greatly in shape from punctate or pustuliform to linear or ramified. Punctate and pustuliform nodules are

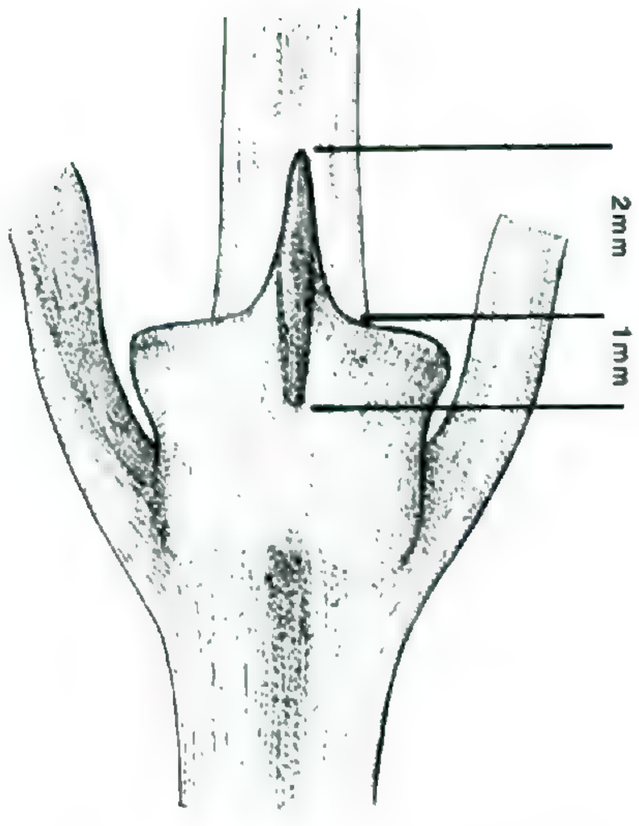


Figure 1. Awned stipule. The awn is defined to include only the upper 2 mm, analogously to a leaf acumen.

usually scattered on blades; linear ones are often along the midrib. Similar nodules are uncommon in other Rubiaceae but are present in 74 African and Madagascan species of *Psychotria* L. and 12 of 17 species of African *Sericanthe* E. Robbrecht (Robbrecht, 1988). In all *Pavetta* species in which nodules occur except *P. urophylla* Bremekamp, they appear on upper leaf surfaces. In *P. urophylla*, like *Psychotria* species, they appear on lower leaf surfaces.

In subgenus *Baconia*, three of Bremekamp's seven series were separated on nodule characters; nodules were variously distributed in his other series. Material observed since Bremekamp's monograph reveals that nodule characters are not consistent enough to assign them as much diagnostic importance as he did. Nodules have been found in all but 2 (*Pavetta rubentifolia* S. D. Manning and *P. molundensis* K. Krause) of the 29 species of subgenus *Baconia* in Cameroon. In nearly half of the species, however, they are sometimes or usually absent. Within specimens, some leaves may reveal a few nodules and others none. In some species, some leaves have profusions of conspicuous nodules while others do not. In most species, most nodules are subpunctate and scattered. In others they tend to be mostly linear and associated with major veins.

Stipules. Single-awned, entire-margined, opposite interpetiolar stipules whose awns are decussate with the leaf pair at the same node are universal in subgenus *Baconia*. Bases of opposite stipules are connate just above petiole bases. Stipules thus sheathe the stem at each node. Stipule awns were measured analogously to leaf acumens, as in Figure 1 in which the awn is cuspidate and 2 mm long. Care must be taken in using awn length diagnostically in subgenus *Baconia*; the tips often break off. In some species stipules are also partly deciduous below their awns.

Inflorescences

Position. Inflorescences in subgenus *Baconia* are almost always terminal on floriferous twiglets, which can be up to 37 cm long. Floriferous twiglets are absent at some nodes, rendering inflorescences at those nodes axillary. Such axillary inflorescences sometimes occur along with terminal ones in collections of *Pavetta camerounensis* S. D. Manning, *P. grossissima*, and *P. tenuissima* made since the second edition of the *Flora of West Tropical Africa* (Hepper & Keay, 1963) and are exceptions to the key to genera of Rubiaceae therein (p. 105), which distinguishes between genera with terminal and axillary inflorescences. At nodes bearing axillary inflorescences, there are typically two oppositely arranged inflorescences. In no species of subgenus *Baconia* are all inflorescences axillary.

Inflorescences are most often solitary but, in some species, some inflorescences are clustered at termini of floriferous twiglets. When inflorescences are so clustered, those on side branches sometimes overtop the central one. Bremekamp (1934) used such overtopping and floriferous twiglet internode lengths to separate three series of subgenus *Baconia* from three others. These characters vary so much within taxa that they are not used diagnostically here.

Architecture. Inflorescences, whatever their shape, are dichasia or modified dichasia which are nearly always compound. Although flowers are usually close enough to each other for corolla lobes of adjacent flowers to overlap, the main branches of inflorescences are sometimes far enough apart that these inflorescences are described as having subunits.

Dimensions and flower number. With rare exceptions, inflorescences are 20 cm or less across. Their sizes and degrees of congestion, though variable within species, are important distinguishing characters between some species.

There are rarely only 1–5 to sometimes more than 400 flowers per inflorescence in subgenus *Baconia*. Flower number is often not a good diagnostic character because within species maximum number of flowers per inflorescence typically is about 10 times the minimum number.

Phenology. Flower opening within an inflorescence usually occurs subsynchronously (flowers toward the center of inflorescences tending to open slightly earlier) after an extended period in full-sized bud.

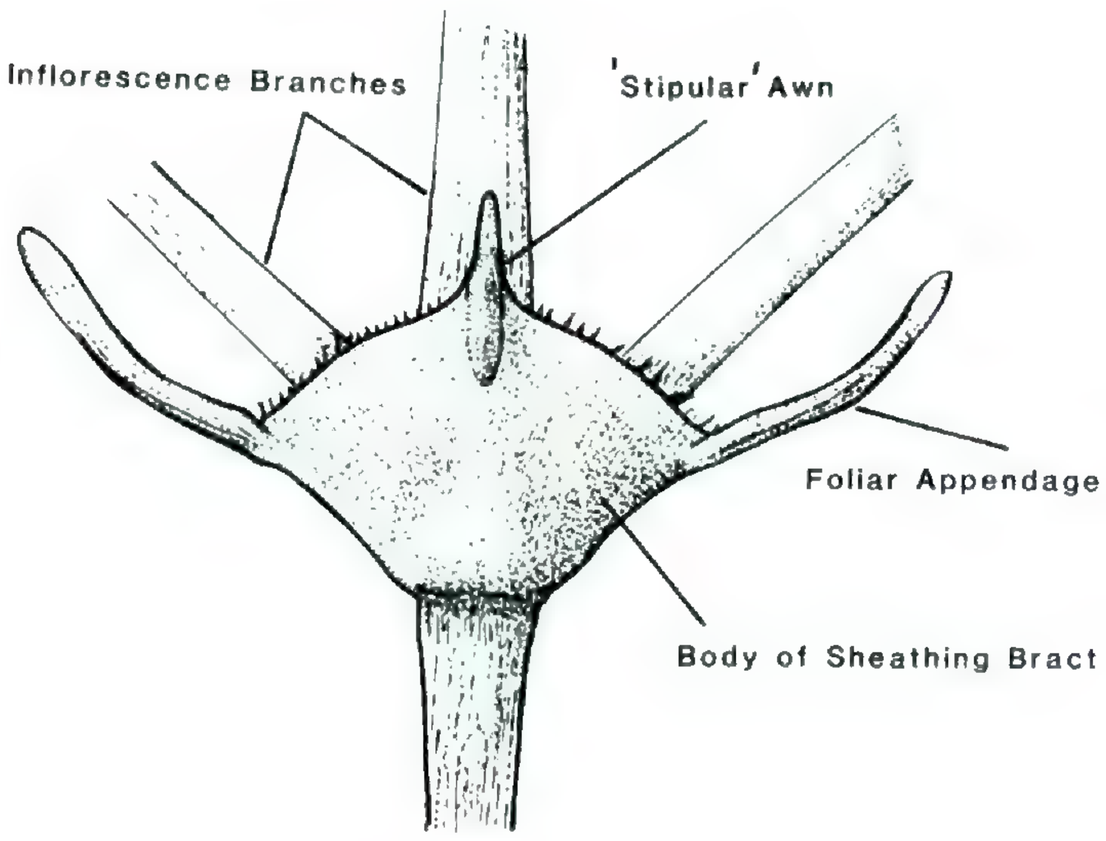


Figure 2. Sheathing bract at base of an inflorescence, showing a normal stipular awn and foliar appendages. The latter look like reduced leaf blades from above or below.

Fruits on an infructescence also usually develop and mature subsynchronously. Sometimes only one or a few fruits develop; often many do. Complete fruits persist on infructescences after ripening.

Bracts, peduncles, and inflorescence delimitation. These features are treated below in some detail either because previous treatments have not done so (bracts) or to clarify or simplify previous treatments (peduncles, inflorescence delimitation). These features have diagnostic value in some species and are used (bracts) or necessary to interpret characters used (peduncles, inflorescence delimitation) in the keys to species.

Bracts. Bracts as described here are of four types: sheathing, foliar, other, and bracteoles.

a. Sheathing bracts. Sheathing bracts are opposite and connate, thus sheathing the axis that bears them. They are present at inflorescence bases and usually also at bases of higher inflorescence branches. They are presumably homologous to stipules, often look like them, and usually bear cuspidate to linear awns in positions one would expect awns on stipules. They sometimes bear additional awns or fimbriae at right angles to the "stipular" position and occasionally in other positions. Numbers and positions of additional bract awns sometimes vary on individual plants. Connation of opposite bracts is often so pronounced that the sheath formed assumes the shape of a cup or, if spreading, of a saucer. At times, sheathing bracts bear foliar appendages. In such bracts the sheathing tissue is adnate to the foliaceous tissue, and the foliar appendages are decussate to the "stipular" position. Such sheathing bracts also bear awns or fimbriae in the normal "stipular" position, and are homologous to a leaf pair and stipule pair. Figure 2 illustrates such a bract.

b. Foliar bracts. Foliar bracts are only sporadically present in subgenus *Baconia*. They are petiolate, unlike foliar appendages on sheathing bracts. Foliar bracts resemble reduced foliage leaves in position and shape, although they are sometimes more reduced in length, proportionately, than in width. They sometimes occur on the main inflorescence axis and sometimes on side branches of the inflorescence subtending flower clusters. Distinctions between foliage leaves, foliar bracts, stipules, and sheathing bracts are illustrated in Figure 3.

c. Other bracts. These are usually more distal in inflorescences than sheathing bracts. They usually range from wedge-shaped to ovate, obovate, or linear and often bear 1–several fimbriae or a tuft of hairs at or near their apices. They can vary considerably in shape within specimens. The largest are distinguishable from sheathing bracts only in that they do not quite sheathe the inflorescence axis. These usually subtend upper inflorescence branches. Smaller ones are usually along side branches. The most reduced ones are fimbriae or awnlike structures on inflorescence branches.

d. Bracteoles. These include all bracts on individual pedicels. They are small and resemble the smaller of the "other bracts" described above. They often take the form of fimbriae as in Figure 4. Their positions on their axes vary. Figure 4 depicts typical variation in nonfoliar bracts and bracteoles.

Peduncles. Little and Jones's (1980) definition of peduncle, in relevant part, is employed here: "the stalk of an inflorescence." The base of the peduncle is at the node of the most apical pair of vegetative leaves and the top is at the point of attachment of the lowermost inflorescence branch. If there is no internode between the most apical vegetative leaves and the lowermost inflorescence branch, the inflorescence is sessile.

Bremekamp's (1934) definition and discussion of peduncles are not followed here because they are more complicated and confusing (Manning, 1990).

Inflorescence delimitation. Whether a branch floriferous twiglet just below the flower cluster terminating a major floriferous twiglet is interpreted as bearing a separate inflorescence or as a branch of a single terminal inflorescence depends on whether the branch has leaves subtending the flower cluster. If so, it bears a separate inflorescence. If not, it is a branch of a single terminal inflorescence. Subtending "leaves" may be considered foliar bracts and the branch a part of a single terminal inflorescence if the "leaves" are reduced more than half in length compared to mature leaves on the main floriferous twiglet just below the inflorescence, or if they are no larger than any foliar

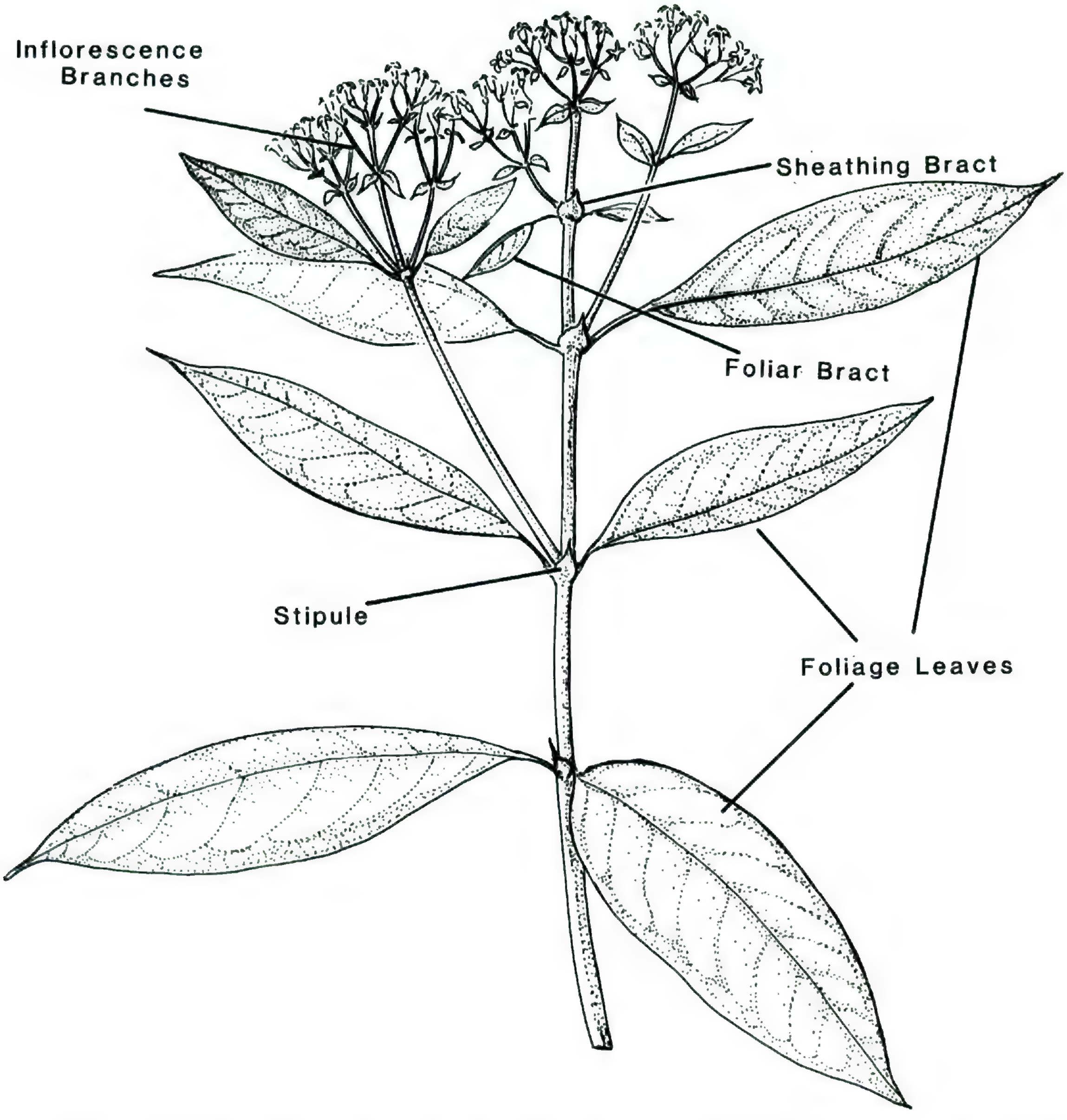


Figure 3. Distinctions between foliage leaves, foliar bracts, stipules, and sheathing bracts in *Pavetta* subg. *Baconia*.

bracts on the main floriferous twiglet rachis, or if they have fallen off and left scars clearly smaller than leaf scars.

The above distinction between solitary and separate inflorescences is only occasionally difficult in practice.

Flowers

Flowers are almost always 4-merous in all species, though occasional 5-merous flowers occur.

Calyx. Calyx tubes in subgenus *Baconia* are often 1–2 mm long. Calyx lobe shape and size are important distinguishing characters, despite variation in most species. Calyx lobes are up to 4 mm long. Typical shapes are illustrated in Figure 5. Although one or two of these shapes predominate in most species, several shapes routinely occur as less common variants.

Calyx lobes in subgenus *Baconia* are usually valvate in open flowers, but often overlapping at the base in bud. Some (never all) lobes remain slightly overlapping at the base in mature flowers in several species. This is used diagnostically for the few species in which it occurs in more than 10% of mature flower calyx lobes.

Corolla. In Cameroon, corollas are usually

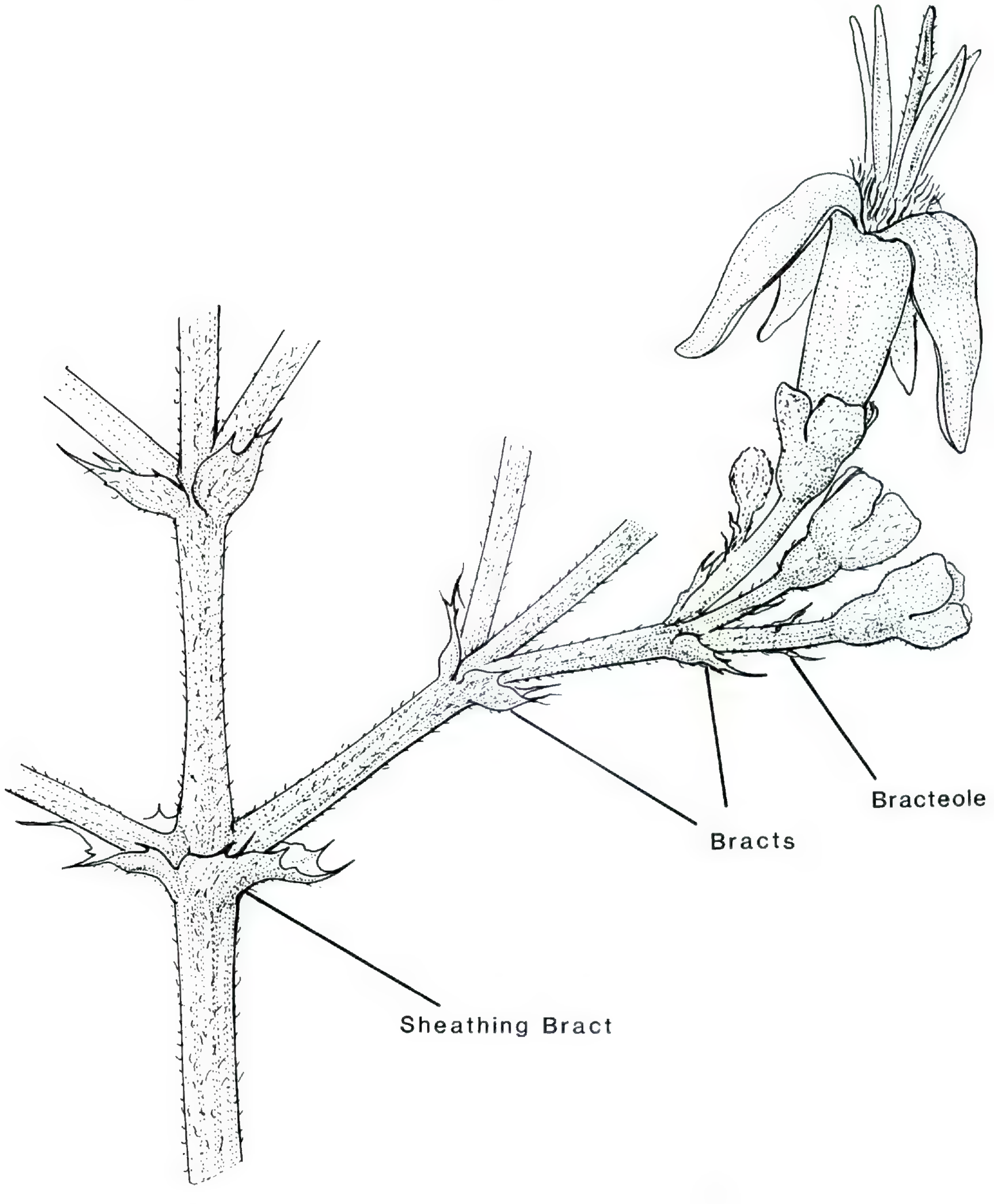


Figure 4. Variation in nonfoliar bracts and bracteoles in *Pavetta* subg. *Baconia*, showing fimbriae.

white, less often greenish white, cream-white, cream, pale green, greenish yellow, yellow, brick red, or with green tips, margins, or stripes.

Corolla exteriors are glabrous; interiors are usually glabrous or subglabrous except the beard of hairs around the corolla throat, attached within the tube near the top. In a few species the beard normally extends unbroken onto the proximal part of the upper surface of the corolla lobes or down into the upper part of the inside of the tube. Rarely, small amounts of shorter vestiture, sharply delimited from the corolla throat beard, also occur on upper surfaces of corolla lobes. In some species, the beard projects outward from the corolla throat.

Members of subgenera *Dizygoön* and *Pavetta* sometimes bear arachnoid vestiture inside upper

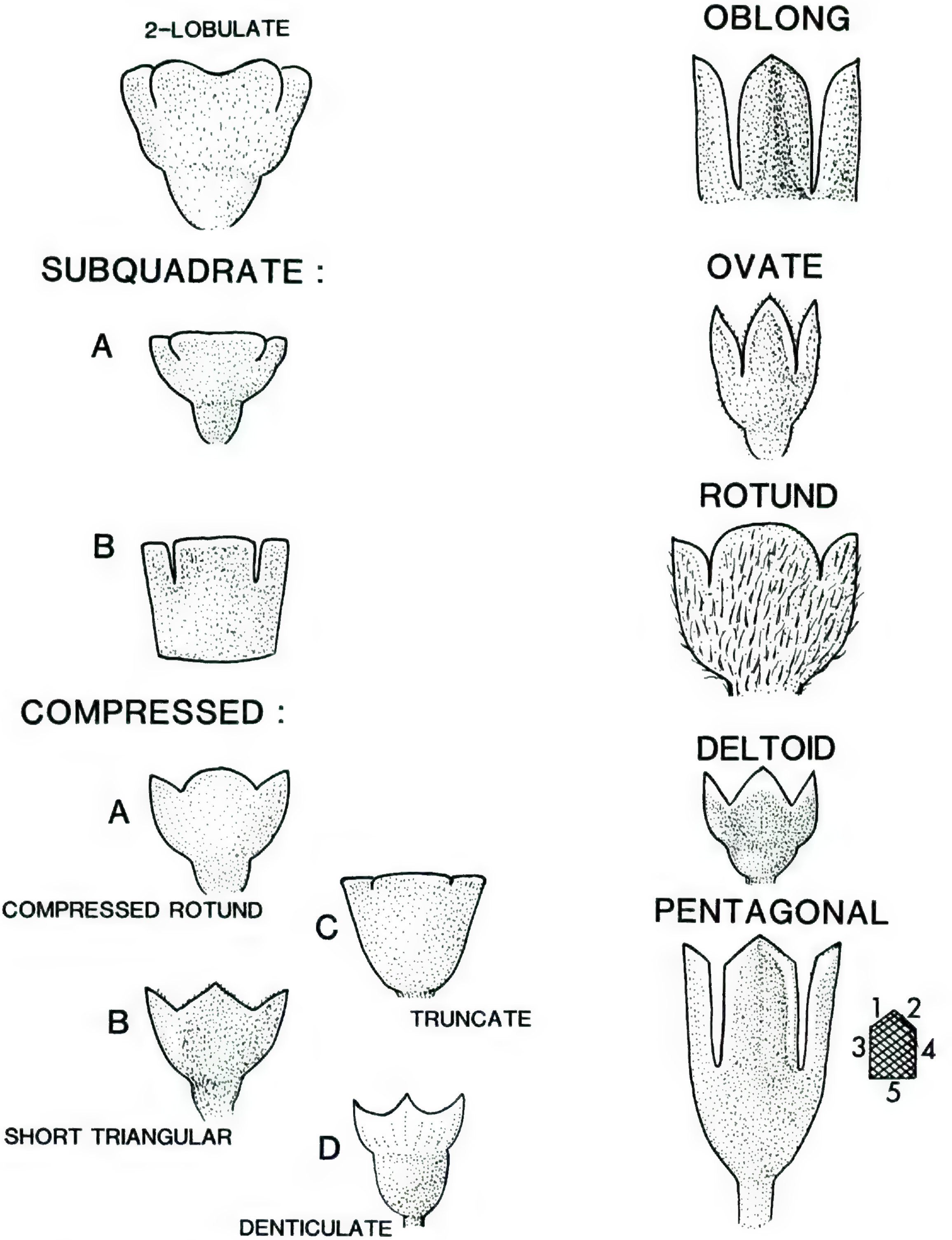


Figure 5. Calyx lobe shapes in *Pavetta* subg. *Baconia*.

parts of corolla tubes. Such vestiture is distinguishable from that of subgenus *Baconia* in at least one of the following three ways: (1) it extends further down into the tube and does not form a distinct ring, (2) it is less dense, or (3) the hairs are finer, shorter, or more curved than the typically bristly hairs of subgenus *Baconia* corolla throats. Corolla throat beards similar to those typical of subgenus

Baconia also occur in some other Rubiaceae, such as the African *Morelia senegalensis* A. Rich. ex DC. and the South American *Isertia coccinea* Vahl.

Corolla tubes vary from cylindrical to twice or more as wide at the top as at the base. A constriction of the tube often occurs just above its base marking a position just above the epigynous nectary disc. Corolla tube length can often be used in distinguishing species despite intraspecific variation. Corolla tubes are normally as short as 2 mm in some species and as long as 10 mm in others. Average corolla tube length in subgenus *Baconia* is about 5 mm, shorter than in subgenus *Pavetta*. The range of variation between longest and shortest tubes in open flowers of most species is about 2 mm. Intraspecific variation seen in this character ranges up to 7 mm; in well collected species whose ranges of variation are probably best represented, longest tubes of open flowers are about twice as long as shortest ones. Corolla tubes are often 1–2 mm wide.

Androecium

a. Stamens. Anthers are introrse, subbasifixed, usually sublinear, and dehisce along longitudinal slits, usually when flowers are in bud. The four stamens are attached to corolla tubes near their throats, alternating with the corolla lobes. When flowers open, anthers become exserted and usually hang down between corolla lobes, sometimes coiling when dry.

b. Pollen. Pollen is tricolporate, globose to subglobose, and typically from 10 to 25 μm in diameter. This is usual in Rubiaceae and tribe Pavetteae (Robbrecht, 1988). Although pollen is usually in monads, tetrads were observed in *Pavetta staudtii* Hutch. & Dalziel (*Zenker 4913*, MO).

Gynoecium

a. Ovary. The inferior ovaries vary from glabrous to pubescent. Vestiture on ovaries is similar to that of inflorescences bearing them until it thins as fruits increase in size. Inside the base of the corolla tube is an epigynous, annular or subannular nectary disc. Structural details are discussed below under "Fruits and Seeds."

b. Style-pollen presenter. Each ovary bears a single, apical style swollen toward its apex. The swollen part is the pollen presenter. Style-pollen presenters range from most often clavate to less often fusiform, and from glabrous to pubescent, sometimes within species. Hairs on pollen presenters are usually suberect, borne nearly perpendicularly from the surface but curved near the apex, and sometimes as long as 0.5 mm. Some species' pollen presenters have clear vertical ridges.

The part of the style below the pollen presenter is normally glabrous in almost all species.

Distances that styles are exserted beyond corolla tubes vary considerably and can be diagnostic at the species level. In some species, styles are exserted over 15 mm; in others, only 3 mm; in most, intermediate distances.

c. Stigma. Stigmas in most species are slightly bifurcated at the tip. They never become recurved as in *Ixora*, however.

Fruits and Seeds

Fruits. Fruits in subgenus *Baconia* are subglobose drupes. A shallow vertical depression around the outside often marks the fruit's division into two locules. Average fruit size ranges from about 5 mm in diameter in some species to about 10 mm in others. Fruits are most often white, off-white, or glaucous, but in some species are orange, orange-green, brown-green, yellow-green, dull yellow, pink, black, bluish black, or white with green vertical stripes; red ones have not been reported.

Fruits in *Pavetta* are divided into two locules by a vertical septum. In almost all species, each locule bears a single ovule from near the midpoint of the septum. Often, both ovules develop into seeds (Fig. 6A). However, sometimes only one of the ovules develops into a seed. This has been observed in over half of species from Cameroon for which fruits are known. Absence of a shallow vertical depression around the fruit exterior often indicates that this has happened. In most such fruits, the septum is close to or against one side of the fruit, resulting in a vestigial locule on the other side of the septum from the developed seed (Fig. 6B).

In *Pavetta camerounensis*, although most fruits have only one ovule per locule as is typical of subgenus *Baconia*, one fruit was seen in which one locule has two seeds borne side by side from a single fleshy placenta whose attachment is near the middle of the septum, while there is only one seed in the other locule (Fig. 6C). This situation occurs more often in *P. lasioclada* (K. Krause) Mildbraed ex Bremekamp, in which it is also common for each of the two locules to bear two seeds (Fig. 6D).

Placentae have been observed to be attached more than halfway up the septum, but never apically, in a few species.

Seeds. Mature seeds occupy most of the volume of their locules. They are nearly hemispherical, except the adaxial side is concave at maturity, with the concavity situated where the placenta was formerly attached. The concavity is typically surrounded by a ringlike outgrowth of testa tissue.

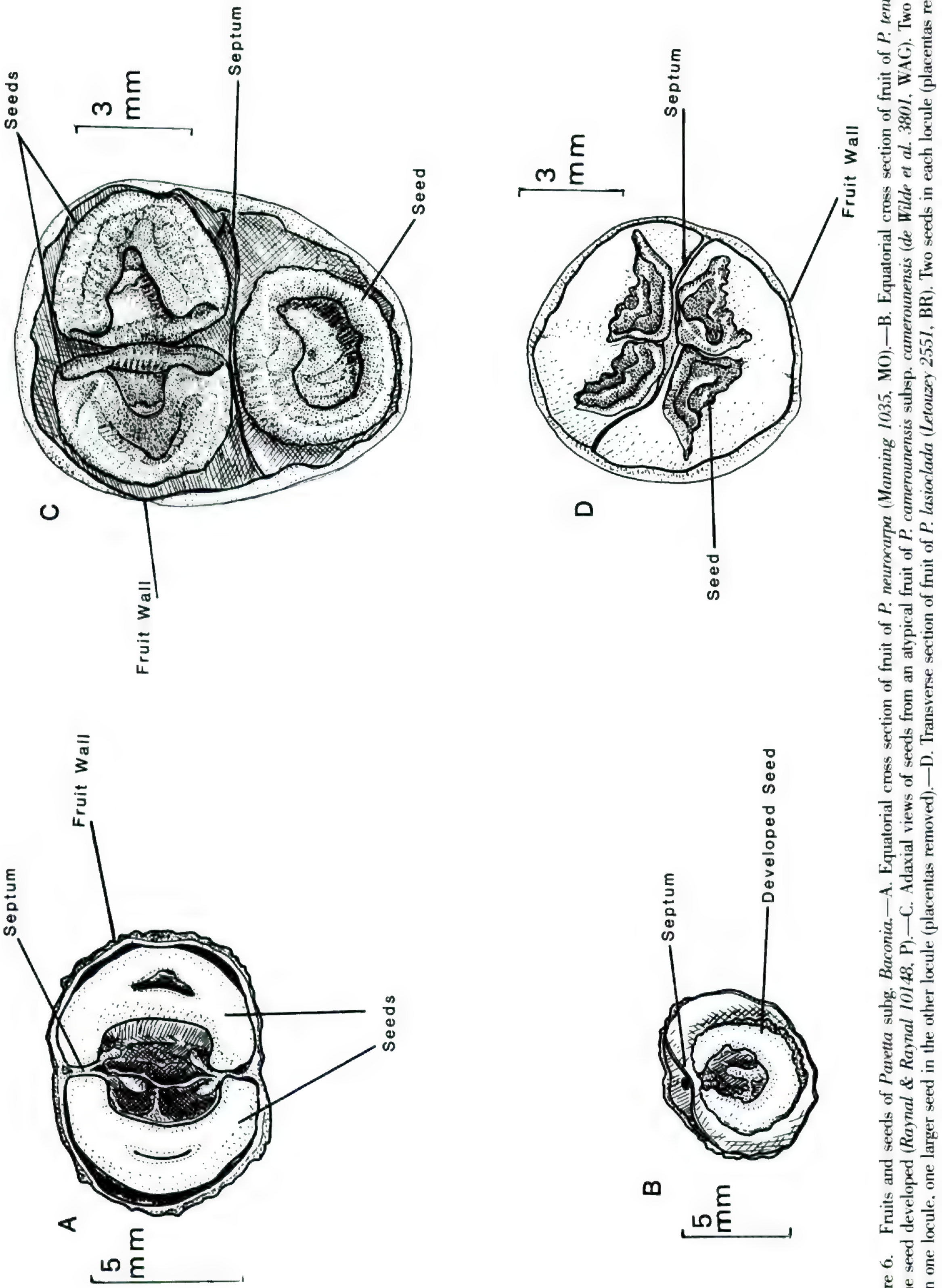


Figure 6. Fruits and seeds of *Pavetta* subg. *Baconia*.—A. Equatorial cross section of fruit of *P. neurocarpa* (*Manning 1035*, MO).—B. Equatorial cross section of fruit of *P. tenuissima*; only one seed developed (*Raynal & Raynal 10148*, P).—C. Adaxial views of seeds from an atypical fruit of *P. camerounensis* subsp. *camerounensis* (*de Wilde et al. 3801*, WAG). Two smaller seeds in one locule, one larger seed in the other locule (placentas removed).—D. Transverse section of fruit of *P. lasioclada* (*Letouzey 2551*, BR). Two seeds in each locule (placentas removed).

Seeds that are less than full sized also occur fairly often in full-sized fruits, however. Rarely, parthenocarpy occurs.

The seeds in four-seeded fruits of *Pavetta lasioclada* (Fig. 6D) are similar to others in the subgenus in basic structure, although constrained to fit within fruits very similar to the two-seeded ones in other species of the subgenus.

Habitat

More species in subgenus *Baconia* have been found in wet forest than in drier forested areas, and more occur in drier forested areas than in savanna. Even in savanna areas, collections are often from gallery forest rather than open savanna.

Reproductive Strategy

Flowers are protandrous. The introrse anthers usually shed pollen onto the swollen upper part of the style (pollen presenter) while the flower is in bud. The pollen presenter becomes exserted as the corolla opens. Pollen adheres to it and is ready for insects to transfer it to receptive stigmas. This pollination syndrome is typical of tribe Pavetteae (Robbrecht, 1984, 1988) and subfamily Ixoroideae (Bremekamp, 1966; Robbrecht, 1988).

March is the peak flowering month for subgenus *Baconia* species in Cameroon. Sixteen of 29 species, and 20 of 38 taxa, including infraspecific taxa, have been collected in open flower in March. This peak flowering is near the beginning of the main rainy season. There have been no flowering collections during September and October, toward the end of the rainy season in much of the forested area, and few during July and August. This cannot completely be accounted for by infrequency of collecting efforts during this wet period; fruits have been collected during every month of the year.

The species with the highest altitudinal range, *Pavetta hookeriana* Hiern, has been collected in flower during more months (August and December as well as February through June) than any other species. It is the most widespread montane species.

Mature fruits of ten species of subgenus *Baconia*. have been collected in Cameroon during November, and those of nine species in December. This peak period for ripe fruits is in the dry season in most parts of the country. In contrast, during the wet month of August, only one species of subgenus *Baconia* has been collected in mature fruit in Cameroon. Intermediate numbers of species have been collected in mature fruit during other months. The spread of fruiting seasons throughout the year is in spite of fewer total species-months being represented in fruiting collections than in flowering collections and no single species having been collected in ripe fruit in more than six months of the year.

Taxonomic Treatment

Taxa in subgenus *Baconia* are morphologically relatively similar and are difficult to separate. Subgenus *Baconia* taxa outside Cameroon show similar amounts and patterns of morphological variation to those in Cameroon. Since species of subgenus *Baconia* are often similar in many characters, one might ask why the whole group or much of it should not be considered a "species complex" as found, for example, by Seyani (1988) in *Dombeya burgessiae* Gerr. ex Harv. & Sond. (Sterculiaceae). This is not done because good correlation of morphology with geographical location has been found in subgenus *Baconia*, while in the *D. burgessiae* complex there was poor correlation of morphology with geography.

Key to Species of *Pavetta* Subg. *Baconia* in Cameroon Based on Characters when Flowering

1. Bacterial nodules on leaves more conspicuous below than above; corollas brick red to beige tan ..... 28. *P. urophylla*
1. Bacterial nodules on leaves more conspicuous above than below, or absent; corollas white, cream, green or yellow 2
2(1). Ovules 2 in both locules of ovary or 2 in one locule, 1 in the other; at least some leaf tertiary veins prominent or prominulous below ..... 14. *P. lasioclada*
2. Ovule 1 per locule; some leaf tertiary veins prominent or prominulous below or not 3
3(2). Some leaf tertiary veins connecting adjacent secondary veins to form a subrectangular gridlike pattern conspicuous below to the naked eye (Figs. 18, 19, 23), leaves without numerous conspicuous light-colored tertiary veins borne from midrib perpendicularly 4
3. Leaf tertiary veins not forming a subrectangular gridlike pattern with secondary veins conspicuous to the naked eye unless tertiary venation also includes numerous conspicuous light-colored veins borne from midrib perpendicularly 6
4(3). Some nonfoliar bracts fimbriate as in Figure 4; inflorescences ca. 6–11 cm across; adaxial surfaces of corolla lobes not pubescent near throat; corolla tubes 5–7 mm long, corolla lobes 6–7 mm long ..... 21. *P. namatae*

4. Most or all nonfoliar bracts lacking fimbriae; inflorescences ca. 0.5–4 cm across; adaxial surfaces of some or all corolla lobes pubescent near throat; corolla tubes 2–5 mm long, corolla lobes 2–6 mm long 5
5(4). Inflorescences ± lax, not subumbellate, (1–)2–4 cm across; average ca. 5–6 veins or veinlets crossed per mm of leaf blade; longest leaf blades ≤18 cm; corolla tubes 3–5 mm long, corolla lobes 4–6 mm long ..... 20. *P. muiriana*
5. Inflorescences congested, subumbellate or with subumbellate subunits, 0.5–2 cm across; average ca. 7 veins or veinlets crossed per mm of leaf blade; longest leaf blades ≥19 cm; corolla tubes 2–3 mm long, corolla lobes 2–4 mm long ..... 27. *P. tenuissima*
6(3). Inflorescences glabrous throughout (or rarely partly subglabrous); nonfoliar bracts almost all lacking fimbriae 7
6. At least part of inflorescences puberulent or pubescent or, if inflorescences glabrous or subglabrous throughout, nonfoliar bracts fimbriate as in Figure 4 8
7(6). Sheathing bracts covering inflorescence branches for most of their lengths (Fig. 13), most sheathing bracts drying light green; inflorescences congested, subumbellate or of tightly clustered subumbellate subunits ..... 12. *P. kribiensis*
7. Sheathing bracts not covering inflorescence branches for most of their lengths, most sheathing bracts drying black or brown; inflorescences congested and subumbellate or not ..... 22. *P. neurocarpa*
8(6). Leaf blades pubescent to subglabrous above (at least a few hairs scattered over the whole upper surface) 9
8. At least part of some or all leaf blades on each specimen glabrous above 11
9(8). Fourth and higher order leaf venation above not obscure when illuminated at 10× ..... 16. *P. longibrachiata*
9. Fourth and higher order leaf venation above obscure when illuminated at 10× 10
10(9). Flowers with corolla lobes longer than corolla tubes; most calyx lobes ovate (Fig. 5), their tips pointed or nearly so; largest leaf blades (11.5–)14.5–22 × 4.5–9 cm; styles exserted 9–11 mm; floriferous twiglets 5.5–19.5 cm long ..... 19. *P. mpomii*
10. Most flowers with corolla lobes shorter than corolla tubes; most calyx lobes subquadrate (Fig. 5) to obovate, their tips not pointed; largest leaf blades (16.5–)21–34 × 8.5–15.5 cm; styles exserted 12–18 mm; floriferous twiglets (6–)18–29 cm long ..... 29. *P. viridiloba*
11(8). Anthers septate ..... 7. *P. cellulosa*
11. Anthers not septate 12
12(11). Leaf apices obtuse to rounded, not acute, most leaf blades oblanceolate or strongly obovate; corolla lobe average length 10–13 mm; average style exsertion 17–23 mm 13
12. Some or most leaf apices acute, most leaf blades elliptical or other shapes but most neither oblanceolate nor strongly obovate; corolla lobe average length ≤9 mm; average style exsertion ≤12 mm 14
13(12). Most calyx lobes short triangular to compressed rotund (Fig. 5), 0.1–1 mm long; corolla lobe average length 10 mm, range 8–13; average style exsertion 17 mm, range 11–20 ..... 13. *P. kupensis*
13. Most calyx lobes deltoid to rotund or pentagonal, not compressed (Fig. 5), 1.5–3 mm long; corolla lobe average length 13 mm, range (9–)12–14; average style exsertion 23 mm, range 20–30 ..... 17. *P. longistyla*
14(12). At least some upper leaf blade surfaces on each specimen appearing dotted when illuminated at 10×, owing to minute papillae 15
14. Upper leaf blade surfaces not appearing dotted or papillate when illuminated at 10× 17
15(14). Corolla tubes (2–)3–8 mm long, corolla lobes (3–)5–9 mm long, styles exserted (2–)6–10 mm ..... 16. *P. longibrachiata*
15. Corolla tubes 1–3 mm long, corolla lobes 2–4 mm long, styles exserted 2–4 mm 16
16(15). Inflorescences congested with ca. 40 flowers per cm of inflorescence width; average corolla tube length 1.5 mm ..... 4. *P. brachysiphon*
16. Inflorescences lax with ca. 10 flowers per cm of inflorescence width; average corolla tube length 3 mm ..... 15. *P. laxa*
17(14). A few hairs scattered over the whole upper leaf blade surface ..... 16. *P. longibrachiata*
17. At least part of some or all leaf blades on each specimen glabrous above 18
18(17). Most calyx lobes subquadrate (Fig. 5) 19
18. Most calyx lobes of shapes other than subquadrate (Fig. 5) 21
19(18). Calyx lobes puberulent externally; nodules, if present, at least as conspicuous on midrib as elsewhere ..... 5. *P. calothyrsa*
19. Calyx lobes glabrous or subglabrous externally; nodules, if present, more conspicuous elsewhere than along midrib 20
20(19). Under 10% of calyx lobe bases overlapping after flowers open, fourth and higher order venation obscure above on most leaves when illuminated at 10×, inflorescences 1–6(–8) cm across with (10–)20–100(–200) flowers ..... 26. *P. staudtii*
20. Over 10% of calyx lobe bases overlapping after flowers open, fourth and higher order venation not obscure above when illuminated at 10× except on some of the largest leaves, inflorescences (4–)7–14 cm across with (75–)100–400 flowers ..... 24. *P. robusta*
21(18). Average calyx lobe length <1 mm 22
21. Average calyx lobe length >1 mm 28
22(21). Average ca. 2 veins or veinlets crossed per mm of leaf blade as seen illuminated at 10× ..... 10. *P. grossissima*
22. Average (3–)4–6 veins or veinlets crossed per mm of leaf blade as seen illuminated at 10× 23
23(22). Longest leaf blades >10 cm including acumen; widest inflorescences always ≥1 cm across 24

23. Longest leaf blades ≤10 cm including acumen; widest inflorescences not always ≥1 cm across ..... 1. *P. baconiella*
24(23). Some inflorescences subcapitate or subumbellate; some or all leaves with >10 pairs of secondary veins ..... 6. *P. camerounensis*
24. Inflorescences not subcapitate; if subumbellate (*P. gabonica*), all leaves with ≤10 pairs of secondary veins 25
25(24). Most calyx lobes subdeltoid to subrotund, not compressed (Fig. 5), their average length 0.75 mm, only occasionally as short as 0.5 mm 26
25. Most calyx lobes compressed (Fig. 5), their average length ≤0.5 mm, only occasionally as long as 0.75 mm 27
26(25). Longest stipule awns ≥5 mm long ..... 2. *P. bidentata*
26. Longest stipule awns <5 mm long ..... 9. *P. gabonica*
27(25). Leaves maroon, stipules glabrous or subglabrous internally, inflorescences 0.5–1.5 cm across ..... 25. *P. rubentifolia*
27. Leaves green, stipules pubescent internally, inflorescences 1–5(–8) cm across ..... 3. *P. brachycalyx*
28(21). Average corolla tube length 3–4 mm, average style exsertion 6 mm 29
28. Average corolla tube length ≥5 mm, average style exsertion ≥8.5 mm 30
29(28). Either most fourth and higher order leaf venation subobscure below when illuminated at 10× or veins intermittently pubescent below as in Figure 12; leaves coriaceous to subcoriaceous ..... 11. *P. hookeriana*
29. Fourth and higher order leaf venation conspicuous below when illuminated at 10×, veins not intermittently pubescent below as in Figure 12; leaves chartaceous to subcoriaceous 16. *P. longibrachiata*
30(28). Over 10% of calyx lobe bases overlapping after flowers open, average calyx lobe length 1.7–2 mm 31
30. Under 10% of calyx lobe bases overlapping after flowers open, average calyx lobe length 1–1.5 mm 32
31(30). Average style exsertion 8.5 mm, range (5–)8–9(–12); nodules absent; veins glabrous below ..... 18. *P. molundensis*
31. Average style exsertion 11 mm, range 9–14; nodules present; veins subglabrous to pubescent below ..... 8. *P. corymbosa*
32(30). Fourth and higher order leaf venation clearly visible above when illuminated at 10× 33
32. Fourth and higher order leaf venation not clearly visible above when illuminated at 10× 35
33(32). Domatia absent along secondary veins below ..... 23. *P. owariensis*
33. Domatia present along secondary veins below 34
34(33). Average ca. 3 veins or veinlets crossed per mm of leaf blade 23. *P. owariensis*
34. Average ca. 4–5 veins or veinlets crossed per mm of leaf blade 16. *P. longibrachiata*
35(32). Fourth and higher order leaf venation obscure or invisible below when illuminated at 10× 23. *P. owariensis*
35. Fourth and higher order leaf venation clearly visible below when illuminated at 10× 36
36(35). Domatia absent along secondary veins below ..... 23. *P. owariensis*
36. Domatia present along secondary veins below ..... 16. *P. longibrachiata*

KEY TO SPECIES OF *PAVETTA* SUBG. *BACONIA* IN CAMEROON BASED ON CHARACTERS WHEN FRUITING (CALYX CHARACTERS INCLUDED)

1. Bacterial nodules on leaves more conspicuous below than above 28. *P. urophylla*
1. Bacterial nodules on leaves more conspicuous above than below, or absent 2
2(1). Seeds 2 in both locules of fruit or 2 in one locule, 1 in the other; at least some leaf tertiary veins prominent or prominulous below ..... 14. *P. lasioclada*
2. Seed 1 per locule; leaf tertiary veins prominent or not below 3
3(2). Some leaf tertiary veins connecting adjacent secondary veins to form a subrectangular gridlike pattern conspicuous below to the naked eye (Figs. 18, 19, 23), leaves without numerous conspicuous light-colored tertiary veins borne from midrib perpendicularly 4
3. Leaf tertiary veins not forming a subrectangular gridlike pattern with secondary veins conspicuous to the naked eye unless tertiary venation also includes numerous conspicuous light-colored veins borne from midrib perpendicularly 6
4(3). Some nonfoliar bracts fimbriate as in Figure 4; infructescences ca. 6–11 cm across 21. *P. namatae*
4. Most nonfoliar bracts lacking fimbriae; infructescences ca. 0.5–4 cm across 5
5(4). Average ca. 5–6 veins or veinlets crossed per mm of leaf blade; infructescences not subumbellate or congested, (1–)2–4 cm across; longest leaf blades ≤18 cm 20. *P. muiriana*
5. Average ca. 7 veins or veinlets crossed per mm of leaf blade; infructescences subumbellate or with subumbellate subunits, congested, 0.5–2 cm across; longest leaf blades >19 cm 27. *P. tenuissima*
6(3). Infructescences glabrous throughout (or rarely partly subglabrous); nonfoliar bracts almost all lacking fimbriae 7
6. At least part of infructescences puberulent or pubescent or, if infructescences glabrous or subglabrous throughout, nonfoliar bracts fimbriate as in Figure 4 8
7(6). Sheathing bracts covering infructescence branches for most of their lengths (Fig. 13), most sheathing bracts drying light green; infructescences congested, subumbellate or of tightly clustered subumbellate subunits ..... 12. *P. kribiensis*
7. Sheathing bracts not covering infructescence branches for most of their lengths, most sheathing bracts drying black or brown; infructescences congested and subumbellate or not ..... 22. *P. neurocarpa*

8(6). Leaf blades pubescent to subglabrous above (at least a few hairs scattered over the whole upper surface) 9
8. At least part of some or all leaf blades on each specimen glabrous above 11
9(8). Fourth and higher order leaf venation not obscure above when illuminated at 10× ..... 16. *P. longibrachiata*
9. Fourth and higher order leaf venation obscure above when illuminated at 10× 10
10(9). Most calyx lobes ovate (Fig. 5), their tips pointed or nearly so; largest leaf blades (11.5–)14.5–22 × 4.5–9 cm; floriferous twiglets 5.5–19.5 cm long ..... 19. *P. mpomii*
10. Most calyx lobes subquadrate (Fig. 5) to obovate, their tips not pointed; largest leaf blades (16.5–)21–34 × 8.5–15.5 cm; floriferous twiglets (6–)18–29 cm long ..... 29. *P. viridiloba*
11(8). Leaf apices obtuse to rounded, not acute; most leaf blades oblanceolate or strongly obovate 12
11. Some or most leaf apices acute; most leaf blades elliptical or other shapes but neither oblanceolate nor strongly obovate 13
12(11). Most calyx lobes short triangular to compressed rotund (Fig. 5), 0.1–1 mm long; domatia present along midrib and sometimes in external angles of two connecting secondary veins of at least larger leaves below; infructescences 2–9 cm across ..... 13. *P. kupensis*
12. Most calyx lobes deltoid to rotund or pentagonal, not compressed (Fig. 5), 1.5–3 mm long; domatia absent; infructescences 9–13 cm across ..... 17. *P. longistyla*
13(11). Mature fruits crowned by persistent calyces most lobes of which are ≥2 mm long 14
13. Mature fruits not crowned by persistent calyces, or persistent calyx lobes <2 mm long 15
14(13). Most calyx lobes subquadrate (Fig. 5) ..... 5. *P. calothyrsa*
14. Most calyx lobes not subquadrate but rather ovate, subrotund or rotund (Fig. 5) ..... 23. *P. owariensis*
15(13). Longest stipule awns >5 mm long; leaves with nodules conspicuous along midrib ..... 2. *P. bidentata*
15. Longest stipule awns ≤5 mm long; leaves with nodules conspicuous along midrib or not—usually not except in *P. hookeriana*, which is variable in this respect 16
16(15). At least some upper leaf blade surfaces on each specimen appearing dotted when illuminated at 10×, owing to minute papillae 17
16. Upper leaf blade surfaces not appearing dotted or papillate when illuminated at 10× 19
17(16). Infructescences congested, ca. 1–3 cm across; calyx lobes longer than wide, their average length ca. 1.0 mm ..... 4. *P. brachysiphon*
17. Infructescences not congested, ca. 0.5–9 cm across; width of calyx lobes subequal to length, their average length 1.1–1.3 mm 18
18(17). Infructescences lax, average length of calyx lobes 1.3 mm ..... 15. *P. laxa*
18. Infructescences neither lax nor congested, average length of calyx lobes 1.1 mm ..... 16. *P. longibrachiata*
19(16). A few hairs scattered over the whole upper leaf blade surface ..... 16. *P. longibrachiata*
19. At least part of some or all leaf blades on each specimen glabrous above 20
20(19). Average ca. 2 veins or veinlets crossed per mm of leaf blade surface as seen illuminated at 10×, mature fruits orange ..... 10. *P. grossissima*
20. Average (3–)4–6 veins or veinlets crossed per mm of leaf blade surface as seen illuminated at 10×, mature fruits orange or not—usually other colors (black, blue, gray, or whitish) in species for which mature fruits are known except in *P. gabonica*, in which they are orange, yellow, or brownish 21
21(20). Leaves maroon, stipules glabrous or subglabrous internally, infructescences ca. 0.5–1.5 cm across ..... 25. *P. rubentifolia*
21. Leaves green, stipules glabrous or subglabrous or not internally, infructescences as narrow as 0.5–1.5 cm or wider 22
22(21). Some infructescences subcapitate or subumbellate; some leaf blades larger than 10 × 2.5 cm including acumen and some or all leaves with >10 pairs of secondary veins ..... 6. *P. camerounensis*
22. Infructescences not subcapitate, in most species not subumbellate either; if subumbellate, either largest leaf blades no larger than 10 × 2.5 cm including acumen or all leaf blades with ≤10 pairs of secondary veins 23
23(22). Fourth and higher order leaf venation not obscure above when illuminated at 10×, or obscure above only on some of the largest leaves 24
23. Fourth and higher order leaf venation obscure above when illuminated at 10× 34
24(23). Average ca. 3 veins or veinlets crossed per mm of leaf blade, fourth and higher order leaf venation easily visible below when illuminated at 10× 25
24. Average ca. 4–6 veins or veinlets crossed per mm of leaf blade, fourth and higher order leaf venation easily visible below or not when illuminated at 10× 26
25(24). Leaf blades not larger than 10 × 2.5 cm including acumen ..... 1. *P. baconiella*
25. Largest leaf blades larger than 10 × 2.5 cm including acumen ..... 23. *P. owariensis*
26(24). Mature fruits orange, yellow, or brownish if known; fourth and higher order leaf venation only moderately easily visible below when illuminated at 10× 27
26. Mature fruits gray, blue-gray, blue-green, whitish green, or blackish if known; fourth and higher order leaf venation easily visible or moderately easily visible below when illuminated at 10× 29
27(26). Hairy pit or pocket domatia up to several mm long along secondary veins of most leaves ..... 7. *P. cellulosa*
27. Domatia not along secondary veins of most leaves 28
28(27). Most calyx lobes deltoid or subdeltoid (Fig. 5), their average length 0.75 mm, only occasionally as short as 0.5 mm; mature fruits orange, dull yellow, or brownish; plants widely distributed but so far not found on Mt. Cameroon ..... 9. *P. gabonica*

28. Most calyx lobes more compressed (Fig. 5) than deltoid, their average length ≤0.5 mm, only occasionally as long as 0.75 mm; fruit color unknown; plants so far found only on Mt. Cameroon ... 3. *P. brachycalyx*
29(26). Fourth and higher order leaf venation easily visible below when illuminated at 10× ... 30
29. Fourth and higher order leaf venation visible but only moderately so or subobscure below when illuminated at 10× ... 33
30(29). Domatia present along secondary veins of most leaves below ... 31
30. Domatia absent or only occasionally present along leaf secondary veins below ... 32
31(30). Fourth and higher order leaf venation more conspicuous above than below ... 7. *P. cellulosa*
31. Fourth and higher order leaf venation not more conspicuous above than below ... 16. *P. longibrachiata*
32(30). Most calyx lobes subquadrate (Fig. 5), nodules scattered on leaf blades, fruits unknown ... 24. *P. robusta*
32. Calyx lobes various, most commonly rotund, most not subquadrate; nodules absent, mature fruits blue-gray or whitish ... 18. *P. molundensis*
33(29). Nodules scattered on leaf blades ... 7. *P. cellulosa*
33. Nodules absent or mostly along midrib ... 11. *P. hookeriana*
34(23). Fourth and higher order leaf venation easily visible below when illuminated at 10× ... 35
34. Fourth and higher order leaf venation not easily visible below when illuminated at 10× ... 37
35(34). Domatia present on secondary veins below as pubescent pits, pockets, or crypts, or veins below puberulent to pubescent ... 8. *P. corymbosa*
35. Domatia not present on secondary veins below as pubescent pits, pockets, or crypts, veins below glabrous or subglabrous ... 36
36(35). Most nodules pustuliform, scattered on blade; most calyx lobes subquadrate (Fig. 5) ... 26. *P. staudtii*
36. Most nodules elongate and associated with secondary or higher order veins; calyx lobes various, often ovate or rotund but most not subquadrate ... 23. *P. owariensis*
37(34). Most nodules pustuliform, scattered on blade; most calyx lobes subquadrate (Fig. 5) ... 26. *P. staudtii*
37. Most nodules not pustuliform; nodules absent or most elongate or associated with midrib or other veins; calyx lobes various but most not subquadrate ... 23. *P. owariensis*

1. Pavetta baconiella Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 73. 1934. TYPE: Cameroon. Between Monjala and Mole, *Mildbraed 8374* (holotype, B destroyed). NEOTYPE: Cameroon. Southwest Province: South Korup National Park, in rocks by Mana River, July 1983 (fl, fl bud & fr), *Thomas 2212* (neotype, MO; isoneotypes, K, P, WAG not seen, YA; 2 other isoneotypes at unknown locations [BR?, PRE?, G?] not seen). Figure 7.

Shrubs 0.8 m. Twiglets glabrous or subglabrous, floriferous twiglets 1–6 cm, 2(–4) of them sometimes growing sympodially to a total length of up to 9 cm, the more proximal inflorescence(s) then pseudoaxillary. Leaves chartaceous, sometimes slightly anisophyllous; blades ovate to elliptical (or less often oblong or obovate), 2–10 × 0.5–3 cm, glabrous except major veins subglabrous or puberulent above and below; apex acute, subacuminate or with acumen 5–15 × 2–3 mm, often curved; base cuneate to attenuate; midrib prominulous below toward base; secondary veins 5–12 each side, usually eucamptodromous, small hairy pit or crypt domatia sometimes in branch vein angles of midrib or secondary veins; nodules scattered on blade, sometimes along midrib, few to many; third and higher order venation ± equally obvious above and below; venation density coarse. Stipules deciduous, cup-shaped, pubescent internally, subglabrous externally, the linear awn to 2 mm. Inflorescences rotund to inverted pyramidal in outline, condensed and subumbellate, 0.2–1.5 cm across, puberulent, sessile, flowers 1–75; sheathing bracts saucer- to cup-shaped, subglabrous, sometimes with a linear awn ca. 3 mm; other bracts to 2 mm, ± ovate to obovate, sometimes with 1–several fimbriae ca. 1 mm; bracteoles ca. 0.5 mm long resembling fimbriae of smaller bracts occasionally borne directly on pedicels. Calyx tube 0.7–1 mm long, 1–1.5 mm wide halfway up; lobes valvate, rotund to deltoid, broadly triangular, subquadrate, pentagonal or ovate, 0.2–0.8 × 0.5–0.8 mm, puberulent, sometimes carinate, rim usually lighter. Corolla yellow; tube cylindrical, 2–3 × 1 mm; lobes 3–5.5 mm; style clavate, subglabrous to pubescent, exserted 3–4 mm. Fruits 5–10 mm across, glabrous or subglabrous. Mature seeds 2 or 1 attached ca. halfway up septum, concave.

Pavetta baconiella was first collected "between Monjala and Mole," Cameroon. This location is unknown. It is otherwise known only from the very high rainfall Korup National Park in Southwest Province, Cameroon. It was found growing in riverside rocks along the Mana River when the river level was probably higher than average.

Leaf size of *Pavetta baconiella* is the smallest of all Cameroon species of subgenus *Baconia*. Sympodial floriferous twiglet growth such as that on some branches of *P. baconiella* has not been seen elsewhere in the subgenus.

The neotype is the only known extant collection of *P. baconiella*.

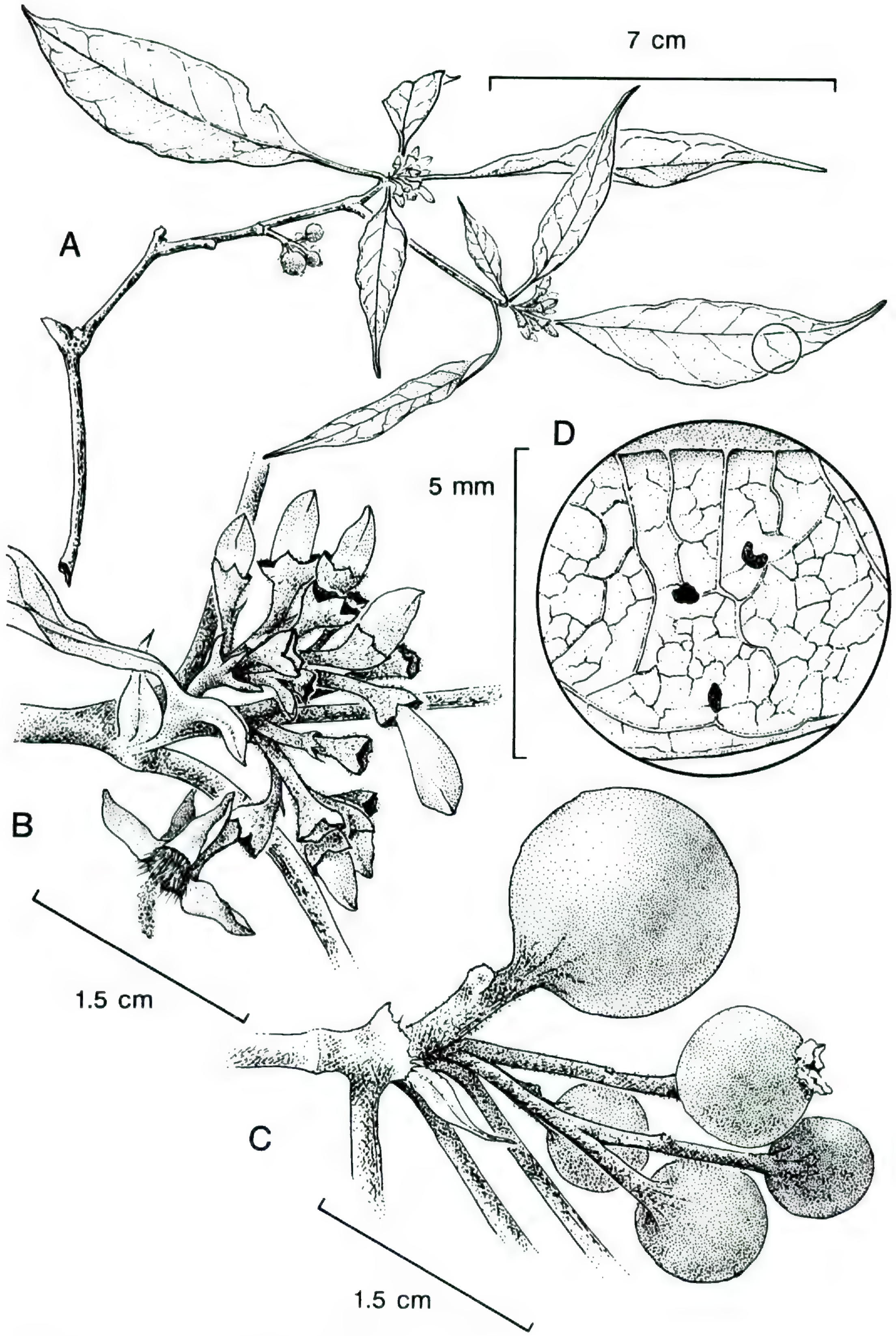


Figure 7. *Pavetta baconiella* (*Thomas 2212*, MO).—A. Habit.—B. Inflorescence.—C. Infructescence.—D. Details of leaf venation and three bacterial nodules on upper leaf surface.

2. Pavetta bidentata Hiern, Fl. Trop. Africa 3: 176. 1877. *Ixora bidentata* (Hiern) Kuntze, Revis. Gen. Pl. I: 286. 1891. TYPE: Equatorial Guinea. Bioko Island, formerly Fernando Po, Apr. 1860 (fl), *Mann 395* (holotype, K).

KEY TO THE VARIETIES OF *PAVETTA BIDENTATA* IN CAMEROON

1. Leaves sessile or subsessile; leaf bases rounded to cordate (or rarely attenuate), some pouched as in Figure 8 ..... var. *sessilifolia*
1. Leaves with petioles to 35 mm long, some always longer than 1 mm; leaf bases cuneate (to less often rounded or attenuate), not pouched ..... var. *bidentata*

a. Pavetta bidentata var. bidentata

Pavetta deistelii K. Schum., Bot. Jahrb. Syst. 33: 353–354. 1903. TYPE: Cameroon. Southwest Province: near Limbe, Jan. 1899 (fl), *Deistel 127* (holotype, B destroyed).

Pavetta permodesta Wernham, J. Bot. 54: 27. 1916. Syn. nov. TYPE: Cameroon. South Province: Bitye, Feb. (fl bud & fl), *Bates 716* (holotype, BM).

Pavetta longistipulata Bremek., Repert. Spec. Nov. Regni Veg. 37: 78. 1934. TYPE: Nigeria. Eket District, 1912–13 (fl), *Talbot & Talbot 3316* (holotype, BM).

Pavetta venusta Bremek., Repert. Spec. Nov. Regni Veg. 37: 78. 1934. Syn. nov. TYPE: Cameroon. Centre Province: Yaoundé, *Mildbraed 7978* (holotype, B destroyed).

Shrubs to 4 m. Twiglets glabrous or subglabrous, floriferous twiglets to 31 cm. Leaves petiolate, petioles to 35 mm; blades coriaceous to chartaceous, sometimes anisophyllous, elliptic to obovate, oblong or ovate, 2.5–31 × 0.7–10.5 cm, glabrous, at times subglabrous below near midrib, veins glabrous; apex acute (or rarely emarginate), sometimes with acumen 3–25 × 1–10 mm; base cuneate to attenuate (or rarely rounded), sometimes asymmetrical; midrib sometimes prominulous below near base; secondary veins 4–18(–22) each side, sometimes joined 1–10 mm from margin; pit, pocket, tuft, or intermediate between pit and crypt domatia usually in branch vein angles of midrib, occasionally in branch vein angles of secondary veins, pubescent, sometimes extending a few mm distally from branch vein angle; nodules usually elongated along midrib; if present on blade, often less frequent than along midrib, sometimes associated with veins; fourth and higher order venation usually more obvious below; venation density medium to fine. Stipules sometimes deciduous; lobes variable including ovate, rotund, compressed rotund, attenuate, deltoid, or pentagonal shapes, or truncate; glabrous; awn linear, 2–15 mm. Inflorescences pyramidal to rotund or corymb-shaped in outline or with subunits of these shapes, 1.5–16 cm across, sometimes lax, puberulent to glabrous, peduncle if present to 15 mm; flowers (1–)10–100(–250); sheathing bracts with rotund, ovate, deltoid, truncate or irregular lobes or unlobed, then funnel- or saucer-shaped, glabrous, at times subglabrous externally, most with narrow awns 0.5–10 mm long, upper ones sometimes with foliar appendages 1–6 mm long; foliar bracts absent or 10–20 mm long. Other bracts linear to pentagonal, ovate, subquadrate, spreading and semicircular, or obovate, to 4 mm long sometimes including 1–several fimbriae to 2 mm long, or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 1–1.8 mm long, 1.5–2 mm wide halfway up; lobes valvate, triangular to rotund (or less often pentagonal, ovate, trapezoidal, subquadrate, compressed rotund (Fig. 5) or 2-pointed); (0.2–)0.5–1 × 0.7–2 mm, glabrous (to occasionally subglabrous), sometimes carinate; rim lighter colored. Corolla white; tube cylindrical or subcylindrical, 4–10 × 1–2 mm; lobes 5–10(–12) mm. Style fusiform to clavate, glabrous to puberulent, exserted 5–15 mm. Stigma narrowly 2-lobed. Fruits to ca. 1 cm across, sometimes with persistent calyx lobes, glabrous, pink or white with green stripes, then blackish. Mature seeds 2 or 1, attached ca. halfway or more up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** Limbe, Apr. (fl), *Maitland 1180* (B, K); Baro, near Korup National Park, Feb. (fl), *Nemba, Thomas & Mambo 889* (MO); Mbu, Rumpi Hills, 10 km W of Wone on Kumba–Mamfe road, Nov. (fl), *Mambo & Thomas 1* (MO), Oct. (fr), *Manning 627* (MO); Etam, Bakossi Forest Reserve, between Kumba and Tombel, Mar. (fl), *Etuge & Thomas 81* (MO) (not *81a*, which is *Pavetta rigida* Hiern); Bakossi Mountains W of Bangem, Jan. (fl), *Thomas & McLeod 5266* (BR, MO), Oct. (fr), *Etuge 335* (MO); Takamanda Forest Reserve, Apr. (fl), *Thomas et al. 7378* (MO). **Littoral Province:** between Njoke and Malende (possibly Southwest Province), Feb. (fl), *Schlechter 12872* (BR, K); 3 km E of Eboné, ca. 10 km S of Nkongsamba, Apr. (fl & vegetative), *Leeuwenberg & Berg 9694* (WAG, YA); and 8 km W of Masok, Apr. (fl), *Leeuwenberg 5414* (K, WAG in part, the other WAG sheet being *P. rigida* Hiern). **Centre Province:** Nkol Bisson, ca. 7 km W of Yaoundé, Jan. (fl bud), *de Wilde & de Wilde-Duyfjes 1689* (P, WAG), Apr. (fl bud & fl), *Breteler 2737* (K, P, WAG), Nov. (fr), *de Wilde & de Wilde-Duyfjes 1208* (P, WAG); hill Akondoi W of Etoug Ebé, Yaoundé, June (fr), *Manning 1916* (MO); Mt. Eloumden, ca. 10 km SW of Yaoundé, Mar. (fl bud), *Sonké 86* (MO), June (fl), *Manning 2123* (MO), June (fr), *Manning 2119* (MO) and *2122* (MO); W of Mt. Fébé, Yaoundé, July (fr), *Manning 2160* (MO); Ngoro, Massif de Ngolé below Banda, NE of Bafia, Apr. (fl), *Raynal & Raynal 10675* (P, YA). **South Province:** Campo Game Reserve, Mar. (fl bud), *Nkongmeneck 469* (BR); Bidjap, 32 km E of Nyabéssan, Mar. (fl bud & fl), *Raynal & Raynal 10283* (P, YA); Lolodorf (fl), *Staudt 212* (S); Bitye (fl bud), *Bates 1318* (MO), Feb. (fl bud & fl), *Bates 716* (BM), month unknown (fl bud & fl), *Bates 1203 & 1318*, combined sheet (BM); hill Ebon, near Nko-

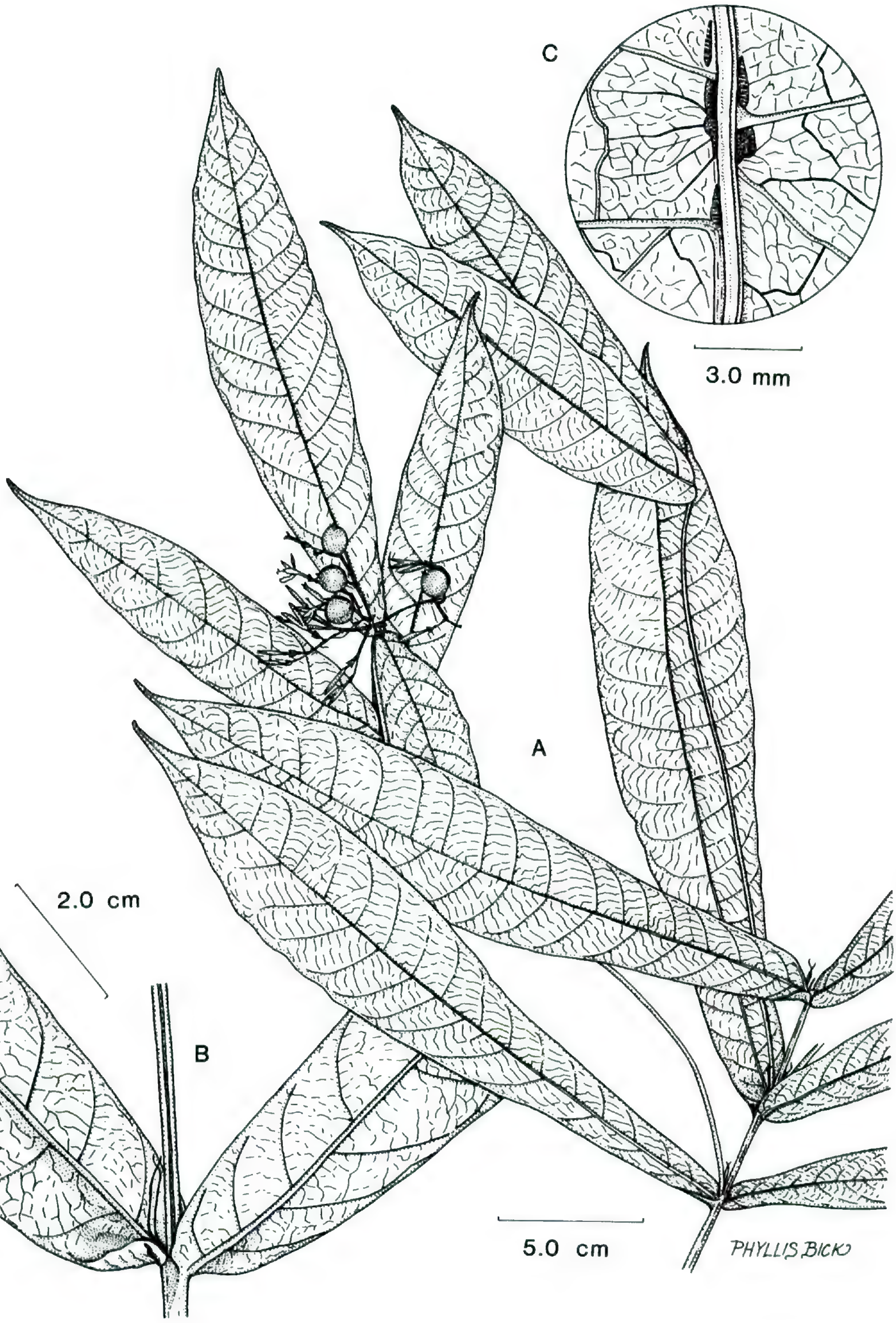


Figure 8. *Pavetta bidentata* var. *sessilifolia* (*Letouzey 11557*, P).—A. Habit, including flowers and fruits on the same inflorescence.—B. Node showing a pouched leaf base and long stipule awns.—C. Details of leaf venation with bacterial nodules along midrib.

biyo, 25 km ENE of Ambam, Mar. (fl bud & fl), *Letouzey 10187* (P). **Unknown Location:** collector unknown, labeled from Herbarium of the Victoria Botanic Gardens (fr), *SCA 2259, HNC 34595* (YA). NIGERIA. **Eket District:** (fl), *Talbot & Talbot 3316* (BM).

b. Pavetta bidentata var. **sessilifolia** S. D. Manning, var. nov. TYPE: Cameroon. Centre Province: hill Kombeng, 8 km SSE of Matomb, ca. 50 km WSW of Yaoundé, July 1972 (fl bud, fl & fr), *Letouzey 11557* (holotype, P; isotype, YA). Figure 8.

A varietate *bidentata* foliis laminis basi plerumque rotundatis ad cordatas, interdum saccatis, petiolis nullis vel ut maximum 1 mm differt.

Similar to variety *bidentata* except full-sized leaves sharply different in being sessile or with petioles ≤ 1 mm and having bases mostly rounded to cordate, sometimes pouched, and not cuneate.

Variety *sessilifolia* is placed within *Pavetta bidentata* because its collections resemble other collections of *P. bidentata* more than any other taxon of subgenus *Baconia*. It is given varietal status because of the sharp differences stated in the last paragraph.

Additional specimen examined. CAMEROON. **Centre Province:** Mt. Kala, 25 km W of Yaoundé, May (fl bud & fl), *Farron 7245* (P).

Pavetta bidentata var. *bidentata* occurs in Zaïre, Equatorial Guinea (Bioko Island), and Nigeria as well as Cameroon, and thus is centered in the Lower Guinean and Congolean subcentres of specific endemism sensu White (1979). In Cameroon, it is widely distributed in Southwest, South, Littoral, and Centre provinces. Variety *sessilifolia* is so far known only from a small area in southern Centre Province, Cameroon.

Pavetta bidentata has been found in primary and secondary forest and at elevations from sea level to as high as 1750 m. Plants collected on rocky or thin-soiled substrates, as well as higher elevation ones, tend to be smaller leaved than those of lowland substrates not reported as rocky.

Aids in recognizing this species are stipule awns usually longer than in other species, often longer than 10 mm; nodules more prevalent along the midrib than elsewhere on leaves; often elongated and pubescent domatia along the midrib; often narrower than average leaves for their length; and, apart from domatia and corolla throats, plants almost completely glabrous.

Several specimens of variety *bidentata* show helicoid inflorescence branching, which is very unusual in subgenus *Baconia*. In variety *sessilifolia*, the terminal leaf pair is sometimes reduced to one leaf, and the leaves of the uppermost two nodes sometimes appear whorled because these nodes are separated by a very short internode.

Pavetta permodesta was a species of unbranched monocaulous dwarfs sensu Robbrecht (1988) whose short stature may have indicated a young stage of the plant, the result of ecological hardship, or having been cut off at ground level. The latter two situations have both been reported on herbarium labels of specimens referred to *P. permodesta*. Features of specimens earlier referred to *P. permodesta* overlap those of other members of *P. bidentata* var. *bidentata*.

Although all material of *Pavetta venusta* seen by Bremekamp (1934) has been destroyed, and no other herbarium material has been found, all *P. bidentata* plants near Yaoundé fit Bremekamp's description of *P. venusta* very well. Their features also overlap with those of other members of *P. bidentata* var. *bidentata*.

3. Pavetta brachycalyx Hiern, Fl. Trop. Africa 3: 169. 1877. *Ixora brachycalyx* (Hiern) Kuntze in Revis. Gen. Pl. 1: 286. 1891. TYPE: Cameroon. Southwest Province: Mt. Cameroon, Dec. 1862 (fl), *Mann 2159* (holotype, K; isotype, P).

Shrubs to 4 m. Twiglets glabrous, floriferous twiglets 4–22 cm. Leaves subcoriaceous, occasionally anisophyllous; blades elliptic to oblong or obovate, (4–)6–20 × (1–)2–9 cm, glabrous, veins glabrous above, glabrous (to less often subglabrous) below; apex acute to obtuse, usually with acumen 5–10 × 3–8 mm; base cuneate to attenuate, occasionally asymmetrical; midrib prominulous or prominent below, secondary veins 4–11 each side, sometimes joined (1–)3–7 mm from margin, sometimes prominulous below; sparingly hairy pocket, pit or crypt domatia in branch vein angles of midrib and occasionally secondary veins; nodules scattered on blade; fourth and higher order venation usually more obvious above; venation density medium. Stipules deciduous, rotund lobed to unlobed and cup-shaped, pubescent internally, glabrous externally, awn cuspidate or linear, ± falcate, 1–4 mm. Inflorescences rotund or subrotund to corymb-shaped in outline or with subunits of these shapes, 1–8 cm across, puberulent distally to subglabrous proximally, peduncle absent or to 7 mm, flowers 10–100. Sheathing bracts with rotund or truncate lobes or unlobed, then bowl-shaped, deciduous, pubescent internally, glabrous (to at times subglabrous) externally, the triangular or linear awns 1–4 × 0.5–1 mm. Other bracts linear to broadly obo-

vate, to ca. 2 mm, usually several-fimbriate, fimbriae ca. 1 mm, or fimbriae borne from axis directly. Bracteoles resembling smaller bracts. Calyx tube 1–1.3 mm long, 1.5–2.5 mm wide halfway up; lobes valvate, compressed rotund (or less often short triangular, rotund or denticulate), 0.2–0.5(–0.8) × 1–1.5 mm (or occasionally truncate at base), subglabrous, sometimes carinate, rim not or narrowly lighter. Corolla creamy white; tube cylindrical or subcylindrical, 3–5(–6) × 1–2 mm; lobes 4–6 mm. Style pubescent, clavate, exserted 5–10 mm. Fruits 7–10 mm across, glabrous, mature color unknown. Seeds 2, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** Mt. Cameroon, Jan. (fl), *Dunlap 20* (K); Mt. Cameroon, Limbe (Victoria) District, Dec. (fl), *TDM = Maitland 908* (K); Mt. Cameroon, S slope above Batoke, Dec. (fl), *Thomas 2827* (MO); Mt. Cameroon, Buea District, Jan. (fl & fr), *Maitland 213* (K).

Pavetta brachycalyx is a forest understory shrub endemic to Mt. Cameroon between ca. 500 and 1500 m. Although specimens with short calyx lobes from other locations have previously been identified as this species, they belong to other species.

Among species with most calyx lobes compressed (Fig. 5), *Pavetta brachycalyx* most closely resembles *P. kupensis* S. D. Manning. *Pavetta kupensis* differs in having mostly strongly obovate leaves and venation often conspicuously brochidodromous below to the naked eye. It also has larger flowers. *Pavetta gabonica* Bremekamp is also similar but has noncompressed calyx lobes.

4. Pavetta brachysiphon Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 74. 1934. TYPE: Cameroon. East Province: near confluence of Lom and Djérem Rivers, near Deng Deng, ca. 235 km NE of Yaoundé, Mar. 1914 (fl), *Mildbraed 8536* (holotype, B destroyed; lectotype, selected here, K).

Shrubs. Twiglets subglabrous, floriferous twiglets 8–20.5 cm. Leaves chartaceous, sometimes anisophyllous; blades elliptic to oblong or obovate, 3–12 × 1–3.5 cm, glabrous below, minutely puberulent or papillate above; veins puberulent to subglabrous below, puberulent above; apex acute with acumen 4–10 × 2–6 mm; base cuneate to attenuate; midrib and secondary veins prominulous below, secondary veins (5–)8–10 each side, sometimes joined 2–6 mm from margin; tuft domatia in branch vein angles of midrib and sometimes secondary veins, sometimes elongated; nodules scattered on blade and sometimes on midrib; fourth and higher order veins more obvious below; venation density fine. Stipules deciduous, sheathing, puberulent externally, pubescent internally; awns not seen. Inflorescences subrotund in outline or with subrotund subunits, 1–3 cm across, congested, pubescent to puberulent, sessile, flowers 50–100; sheathing bracts subrotund lobed to cup-shaped without lobes, pubescent internally near base, puberulent to subglabrous externally; sheath with linear awns or foliar appendages to 2 mm; other bracts deciduous, subquadrate to subquarter-spherical or ovate, to 2 mm, sometimes with 1–many fimbriae to ca. 1 mm; bracteoles resembling smaller bracts. Calyx tube 0.5–0.8 mm long, 1.2–1.8 mm wide halfway up; lobes valvate, rotund to oblong, ovate or pentagonal, 0.5–1.5 × 0.5–1 mm, puberulent, often carinate, rim lighter. Corolla tube cylindrical, 1–2 × 1 mm; lobes 2–4 mm. Style clavate, subglabrous, exserted 2–4 mm.

Pavetta brachysiphon is known only from the type specimen from northwestern East Province, Cameroon, near a forest-savanna boundary. Although the calyx lobes of *P. brachysiphon* are of approximately average length in subgenus *Baconia*, *P. brachysiphon* is distinguished by its otherwise very small flowers in very congested inflorescences. Leaves are small and narrow. The following aspects of leaf morphology are also distinctive: leaves are more or less papillate on upper surfaces and tend to dry golden brown below, darker brown above; domatia are usually along lateral veins as well as the midrib; and fine venation tends to be more obvious below than above. *Pavetta longibrachiata* Bremekamp, *P. laxa* S. D. Manning, and *P. cellulosa* Bremekamp are three species similar to *P. brachysiphon* in these aspects of leaf morphology, except fine venation tends to be more obvious above than below in *P. cellulosa*.

5. Pavetta calothyrsa Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 69. 1934. TYPE: Cameroon. East Province: 3°45′–4°N, between "Lamoko" and the "Posten Plehn," formerly Bezirk Molundu, probably near Ndélélé, Apr. 1911 (fl), *Mildbraed 4921* (holotype, B destroyed; lectotype, selected here, HBG).

Shrubs to 4 m. Twiglets glabrous, floriferous twiglets (6–)20–27 cm. Leaves coriaceous, glabrous, occasionally anisophyllous; blades elliptic to ovate (or less often rotund, oblong, or obovate), (5–)9–32(–37) × 3–13 cm; apex acute to obtuse or rounded, usually with acumen 5–20 × 3–15 mm; base cuneate to attenuate, sometimes asymmetrical; midrib and secondary veins sometimes prominulous below; secondary veins (5–)7–10(–11) each side, usually eucamptodromous; small, subglabrous pit or pocket

domatia sometimes in branch vein angles of midrib; nodules uncommon, usually limited to midrib if present; fourth and higher order veins usually slightly more obvious below, at least somewhat obscure on both faces; venation density fine. Stipules sometimes deciduous, cup-shaped, glabrous externally, pubescent (to rarely subglabrous) internally, the sometimes deciduous linear to triangular awn ca. 3–8 mm. Inflorescences subrotund to corymb-shaped or with subunits of these shapes, 3–25 cm across, pubescent to glabrous; peduncles absent or to 20 mm; flowers 35–450; sheathing bracts sometimes deciduous, lobes broadly triangular to rotund or unlobed, sheath then saucer- or cup-shaped, puberulent to glabrous externally, pubescent or puberulent internally, sometimes with linear awns 1–7 mm or foliar appendages 2–23 mm, foliar bracts similar to slightly reduced foliage leaves occasionally present, other bracts wedge-shaped to ovate, obovate or linear, sometimes truncate or deltoid at top, lobed, or with 1–several fimbriae to 1 mm long at top or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 1–1.5 mm long, 2–2.5 mm wide halfway up; lobes valvate (or less often overlapping slightly at the base), subquadrate, shallowly 2-lobulate (or less often rotund), 0.5–1.5(–2) × 1–2 mm, puberulent, often carinate, rim sometimes lighter. Corolla white, whitish green, or white with greenish apex; tube cylindrical except often constricted at or near base to ca. half its diameter above, 5–9 × 2–4 mm; lobes 5–12 mm, sometimes reflexed. Style clavate, pubescent to puberulent, exserted 8–15 mm. Stigma sometimes narrowly 2-lobed. Fruits 7–10 mm across, crowned by slightly accrescent persistent calyx, subglabrous to glabrous, whitish green. Mature seeds 2 or 1, attached ca. halfway or more up septum, concave.

Additional specimens examined. CAMEROON. **East Province:** Boyo River W of Kongolo near Bétaré Oya, Feb. (fl bud), *Letouzey 3533* (BR, P, YA); 5 km E of Bertoua, Dec. (fr), *Breteler 790* (WAG); 5 km E of Moloundou, Apr. (fl), *Villiers 692* (P); River Dja between Ntouo and Meu Rivers, near Abong Mbang, Apr. (fl), *Letouzey 3763* (BR, YA). **South Province:** Bitya, near River Dja (fl), *Bates 1821* (K), *1822* (K); Avébé Esse, 25 km W of Sangmélima, Mar. (fl), *Letouzey 10145* (BR, P, YA). **Centre Province:** Yaoundé, Jan. or Feb. (fl bud), *Mildbraed 8014* (HBG, K), month unknown (fl bud & fl), *Zenker 700* (NY, K upper part of sheet, P, S), month unknown (fl), *Zenker s.n.* (NY), *Zenker & Staudt 269* (W); N'Kolbisson, 8 km W of Yaoundé, Nov. (fr), *de Wilde & de Wilde-Duyfjes 1217* (BR, MO, WAG, YA); Ngoro, 28 km NE of Bafia, Mar. (fl bud & fl), *Raynal & Raynal 10557* (P, YA); Massif de Ngolé near Ngoro, Apr. (fl), *Raynal & Raynal 10713* (P, YA); and Colline d'Ebat, 40 km SSW of Bafia, Dec. (fl bud), *Letouzey 9692* (BR, YA). **West Province:** Bangang-Fokam, 10 km NE of Bangwa, Apr. (fl bud & fl), *de Wilde & de Wilde-Duyfjes 2378* (MO, BR, WAG, YA); Mt. Bana, Jan. (fl), *Félix 2994* (P).

The northwest portion of the known range of *Pavetta calothyrsa* is in Cameroon, where it occurs in widely scattered drier areas of forest in East, South, Centre, and West Provinces. The species has also been reported from Gabon and Zaïre. It is commonly found in gallery forest and sometimes in or on the edge of forest in otherwise savanna areas, or in disturbed areas. It has been reported on marshy black humus and rocky substrates. Reported elevations are from 650 to 1400 m.

The inflorescences of *Pavetta calothyrsa* are usually among the largest, and peduncles are sometimes among the longest, in subgenus *Baconia.* Most leaves and flowers are also larger than average for the subgenus. The only other taxon of subgenus *Baconia* from Cameroon whose fruits are known to have conspicuously large, persistent calyx lobes is *P. owariensis* Palisot de Beauvois var. *satabiei* S. D. Manning, in which they are rotund to deltoid, pentagonal, or ovate but not subquadrate or 2-lobulate as in *P. calothyrsa. Pavetta calothyrsa* and *P. molundensis* are superficially similar but differ in calyx lobe shape. *Pavetta calothyrsa* resembles *P. robusta* Bremekamp in calyx lobe shape, large leaves, and many-flowered inflorescences, but calyx lobes in *P. calothyrsa* are 1 mm or more long, those in *P. robusta* 0.5–1 mm long. Also, bacterial nodules are absent or few and usually along the midrib in *P. calothyrsa*; in *P. robusta*, they are scattered on the blade more than along the midrib.

Pavetta calothyrsa is restored here from synonymy with *P. nitidula* Hiern, which does not occur in Cameroon. *Pavetta calothyrsa* and *P. nitidula* are similar (Hiern, 1898; Bridson, 1978), but *P. nitidula* has sessile or subsessile leaves only 3.5–16.5 × 1–4.5 cm lacking acumens, usually triangular or rotund calyx lobes, sometimes purple or pink corollas, many more nodules including some scattered on the blade, and inflorescences only 2–7 cm across.

6. Pavetta camerounensis S. D. Manning, sp. nov. TYPE: Cameroon. South Province: massif de Ngovayang, 16 km W of Lolodorf, Feb. 1979 (fl bud & fl), *Satabié & Letouzey 373* (holotype, P; isotype, YA).

KEY TO THE SUBSPECIES OF *PAVETTA CAMEROUNENSIS* IN CAMEROON

1. Floriferous twiglets 9–21 cm long
   subsp. *camerounensis*
1. Floriferous twiglets absent or 0.5–9 cm long
   subsp. *brevirama*

a. Pavetta camerounensis subsp. **camerounensis.** Figure 9.

Frutices. Rami glabri (vel aliquando subglabri). Rami floriferi 9–21 cm. Folia nervis secundariis utroque 8–23, domatiis nullis, aliquot venis tertiariis interdum subter prominentibus vel prominulis. Inflorescentiae 0.2–2.5 cm latae, saepe congestae. Lobi calycini valvati, subrotundati (ad interdum rotundatos, triangulares, denticulatos vel truncatos), ≤ 1 × 1–1.5 mm, glabri. Corolla tubo 2–4 mm, lobis 3–5 mm, lobis saepe super prope faucem puberscentibus. Styli exserti 2–4 mm. Semina 1–2(–3).

Shrubs to 2.5 m. Twiglets glabrous (to at times subglabrous), floriferous twiglets 9–21 cm. Leaves chartaceous to coriaceous, glabrous (to less often puberulent on veins below), occasionally anisophyllous; blades broadly to narrowly obovate, elliptical, ovate (or occasionally oblong), 12–32 × (2.5–) 4–12 cm; apex acute to obtuse or rounded usually with acumen 5–30 × 2–10 mm; base cuneate to attenuate, sometimes asymmetrical; midrib and secondary veins prominent or prominulous below at least near base, secondary veins sometimes impressed above, 8–23 each side, usually joined 1–11 mm from margin; domatia absent; nodules absent or few, linear, along midrib and secondary veins or rarely on blade; tertiary veins sometimes prominulous below; fourth and higher order venation obvious above and usually below; venation density medium. Stipules often deciduous or fragmented, apparently rotund to ovate or deltoid lobed, glabrous or subglabrous (or less often puberulent) externally, glabrous to thinly pubescent especially near base internally, at least sometimes with a linear or cuspidate awn 1–5 × 1–3 mm. Inflorescences sometimes subcapitate or subumbellate, rotund to subrotund in outline, 0.2–2.5 cm across, congested, puberulent to glabrous, peduncle absent or to 3 mm, obscured by sheathing bracts, flowers 5–60; sheathing bracts rotund to deltoid lobed or unlobed, then saucer- or bowl-shaped, glabrous to puberulent or thinly pubescent, sometimes with ovate or linear awns or foliar appendages 1–3 mm long, sometimes attached ca. halfway down the sheath, sometimes near its apex; other bracts often light cream, subquadrate to subtruncate and wedge-shaped, ovate, deltoid or linear, often at least as wide as long, to 2 mm, sometimes including 1–3 fimbriae or a linear awn ca. 1 mm, or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 0.7–1 mm long, 1.2–2 mm wide halfway up; lobes valvate, compressed rotund (to less often truncate, rotund, triangular, denticulate or cleft near apex), ≤ 1 × 1–1.5 mm, glabrous, sometimes carinate, rim lighter, sometimes narrowly so. Corolla white, creamy, pale green, or greenish yellow; tube cylindrical or subcylindrical, sometimes constricted near base, 2–4 × 1–2 mm; lobes 3–5 mm, usually puberulent near base above. Style fusiform or clavate, pubescent to subglabrous, exserted 2–4 mm. Fruits 7–12 mm across, sometimes with persistent calyx, glabrous, dirty or glaucous grayish green, bluish, or greenish white with a bluish sheen. Mature seeds 1–2(–3), attached halfway or more up septum, concave.

Additional specimens examined. CAMEROON. **South Province:** Bipindi, Jan. (fl), *Manning 1408* (MO); hill Nkoltsia ca. 23 km NW of Bipindi, Nov. (fl bud), *Villiers 1003* (P); 27 km E of Kribi, Jan. (fl), *Bos 6173* (K, P, WAG); and 10 km E of Kribi, May (fr), *Bos 4654* (WAG). **Centre Province:** N'kolbisson, 8 km W of Yaoundé, Nov. (fl bud & fl), *de Wilde & de Wilde-Duyfjes 1211* (WAG), Nov. (fr), *de Wilde & de Wilde-Duyfjes 1184* (P, WAG), Sep. (fr), *Manning 171* (MO); Mt. Fébé, near Yaoundé, Nov. (fr), *de Wilde et al. 3801* (WAG); 15 km SSW of Obala, Dec. (fl), *Letouzey 9776* (BR, YA). **Centre or Littoral Province:** Kéllé River, 60 km NNW of Eséka, Mar. (fr), *de Wilde & de Wilde-Duyfjes 2186* (P, WAG); Kéllé River 50 km NW of Eséka, Nov. (fl bud & vegetative), *de Wilde & de Wilde-Duyfjes 1318 & 1318B* (WAG), *1318C* (P); not *1318* (K) & *1318C* (WAG), which are *Pavetta gabonica*; 30 km WNW of Eséka, Dec. (fl bud & fr), *de Wilde & de Wilde-Duyfjes 1491* (BR, WAG). *De Wilde & de Wilde-Duyfjes 1318* is a mixed collection; *1318*, *1318B*, and *1318C* above refer to designations on herbarium labels, not tied tags attached to specimens, when the designations conflict.

b. Pavetta camerounensis subsp. **brevirama** S. D. Manning, subsp. nov. TYPE: Cameroon. Southwest Province: Barombi-Mbo village, ca. 5 km NW of Kumba, Dec. 1986 (fl bud & fl), *Nemba & Thomas 417* (holotype, MO; isotypes, BR, YA not seen). Figure 10.

A subspecie *camerounensi* ramis floriferis absentibus vel non plus quam 9 cm longis, inflorescentiis interdum axillaribus differt.

Similar to subspecies *camerounensis* except floriferous twiglets absent or less than 9 cm long, inflorescences sometimes axillary with peduncle to 5 mm.

Although the longest floriferous twiglet of subspecies *brevirama* is as long as the shortest in subspecies *camerounensis*, floriferous twiglets of the two subspecies normally differ sharply in length (Figs. 9 and 10). Although other character states overlap, the following features of subspecies *brevirama* also tend to differ and may be useful in confirming identifications: absence of leaves with broadly ovate blades (common in subspecies *camerounensis*) or rounded apices, though other shapes described for subspecies *camerounensis* all occur; nodule-like growths if present sometimes ramifying extensively with leaf ve-

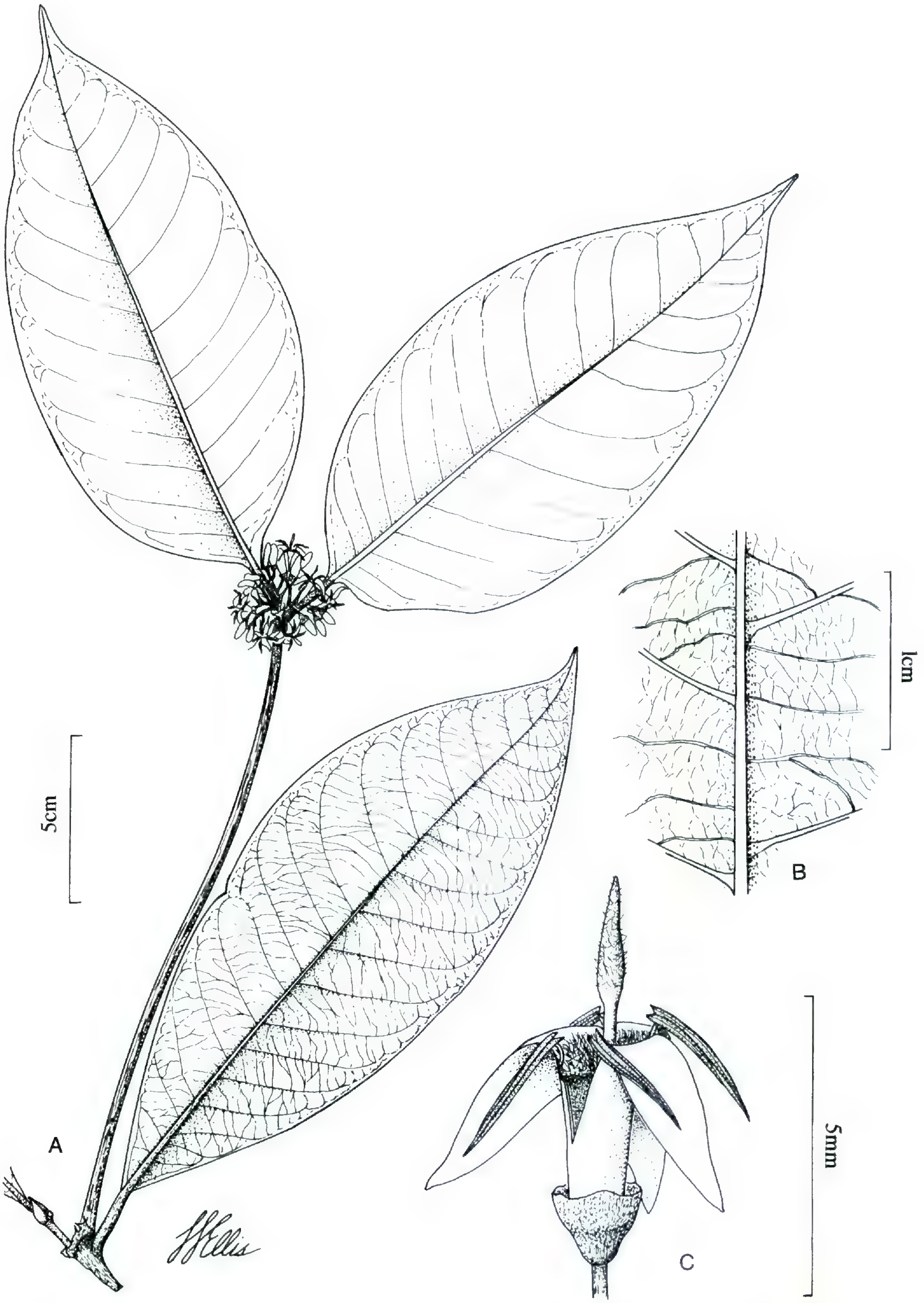


Figure 9. *Pavetta camerounensis* subsp. *camerounensis* (*Satabié & Letouzey 373*, P).—A. Habit.—B. Details of leaf venation.—C. Flower.

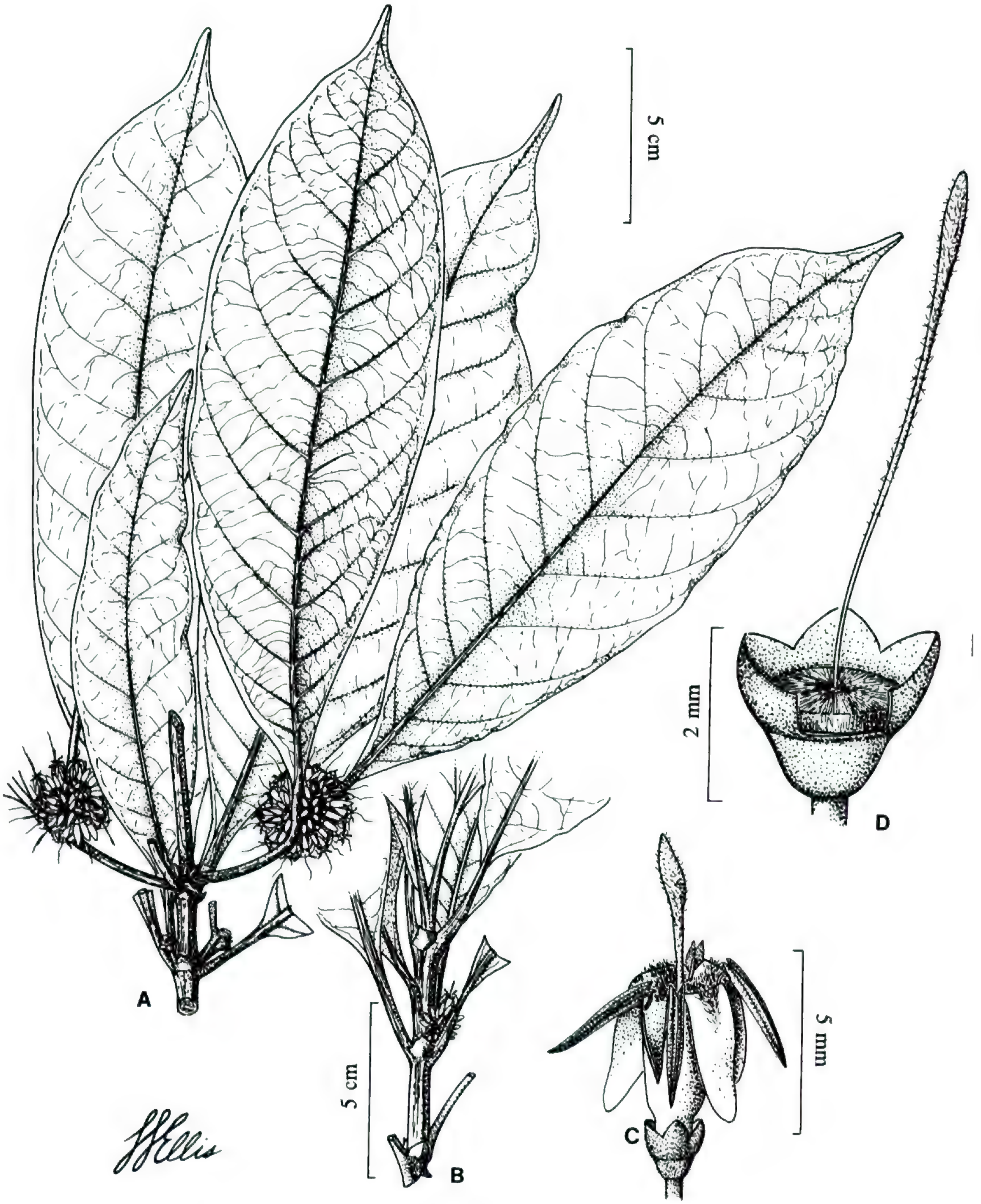


Figure 10. *Pavetta camerounensis* subsp. *brevirama* (*Nemba & Thomas 417*, MO). (A, C, D, MO holotype; B, MO isotype).—A. Habit—larger inflorescences terminal on short side branches, smaller ones axillary at lower nodes.—B. Nodes, one showing an axillary inflorescence.—C. Flower with corolla throat beard extending out onto corolla lobe.—D. Flower, corolla and part of calyx removed to show epigynous nectary disk.

nation; sheathing bract awns sometimes up to 5 mm; other bracts sometimes obscured by inflorescence congestion; calyx lobes occasionally subquadrate, sometimes puberulent; major veins rarely impressed above. Subspecies *camerounensis* specimens often dry lighter green than those of subspecies *brevirama*. Also, the two taxa are largely geographically separate.

Additional specimens examined. CAMEROON. **Southwest Province:** Korup National Park, Mar. (fl & young fr), *Thomas & McLeod 5724* (MO), Dec. (fl bud & fr), *Thomas 4108* (MO), Apr. (young fr), *Manning 1742* (MO), *1750* (MO), Apr. (young fr & fr), *Manning 1757* (MO), Apr. (fr), *Manning 1729* (MO); Ekondo Titi-Mundemba road, Jan. (fl), *Thomas 4358* (MO); S of Ekumbako, Dec. (fl bud, fl & fr), *Thomas 2703* (MO); Mundemba-Fabe road, Nov. (fr), *Nemba 336* (MO); Southern Bakundu Forest Reserve, Banga, Mar. (young fr), *Brenan 9279* (K), *9279A* (K), W of Bombe, Sep. (fr), *Manning 101* (MO), *111* (MO), A.T.S.S. plot 2A, Aug. (fr), *Olorunfemi FHI 30719* (K); inside crater of Lake Barombi-Mbo, ca. 3 km NW of Kumba, Nov. (fl bud & fl), *Manning 854* (MO), Nov. (fl & fr), *Manning 849* (MO), *856* (MO); 1 km W of Lake Barombi-Mbo, ca. 5 km NW of Kumba, Dec. (fl & fr), *Manning 1080* (MO); Bolo-Meboka, Kumba-Mamfe road between Kumba and Konye, Sep. (fr), *Nemba 245* (MO); Baduma, Kumba-Mamfe road, Aug. (fr), *Nemba & Thomas 185* (MO); Bakolle-Bakossi, Kumba-Mamfe road, May (fr), *Etuge & Thomas 134* (MO). **Littoral Province:** Douala–Yabassi road 30 km N of bifurcation for Edéa, May (fr), *Farron 7286* (P).

So far as is known, both subspecies of *Pavetta camerounensis* are endemic to Cameroon. Subspecies *camerounensis* has been found only in the wet western portion of South Province and in southern Centre and (?) Littoral Provinces. Subspecies *brevirama* is one of the most common *Pavetta* taxa in and near the extremely high rainfall Korup National Park in southwestern Southwest Province. It also occurs north and east of there in less extremely wet forest in Southwest and Littoral Provinces.

Subspecies *camerounensis* is a shrub at elevations from 120 to 1000 m in varied habitats, usually in fully shaded forest. It also occurs in degraded and secondary forest and forest borders and has been collected both along rivers and on mountains. Reported substrates include sandy and clayish soils and loamy soil on granitic rock. Subspecies *brevirama* is a small shrub in deep shade and less often partly shaded locations. Its highest reported elevation is 350 m, inside the crater of Lake Barombi Mbo, not far above lake water level.

Corolla throat vestiture of *Pavetta camerounensis* extends onto adaxial surfaces of corolla lobes, a condition found in only a few other species. *Pavetta camerounensis* resembles *P. grossissima*, *P. gabonica*, and *P. tenuissima*. *Pavetta camerounensis*, like *P. grossissima*, has inflorescences so condensed as to often appear subumbellate; *P. grossissima*, however, has extremely coarse reticulation of higher order leaf venation, unlike *P. camerounensis*. The largest inflorescences of *P. camerounensis* resemble those of *P. gabonica*, but in *P. gabonica* the corolla throat vestiture does not normally extend onto the lobes as it does in *P. camerounensis*. The number of secondary vein pairs does not exceed 10 in *P. gabonica*; it always does on at least some leaves in *P. camerounensis*. Specimens of *P. gabonica* often have smaller leaves than those of *P. camerounensis*. *Pavetta camerounensis*, particularly subspecies *brevirama*, resembles *P. tenuissima* in its condensed inflorescences, leaf sizes and shapes, lack of anisophylly, and in that floriferous twiglets are sometimes so reduced as to render inflorescences axillary. *Pavetta tenuissima* differs in that its leaves usually have extremely fine mesh reticulation of their higher order veins and in that its secondary and tertiary veins have a more predominant rectangular gridlike pattern below on herbarium specimens.

Pavetta camerounensis is so named because it is relatively widespread in Cameroon forests.

7. Pavetta cellulosa Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 75. 1934. TYPE: Zaïre. Eala, Sep. 1907 (fl bud & fl), *Pynaert 1692* (holotype, BR).

Shrubs or small trees with stem to at least 5 cm diam. Twiglets subglabrous or glabrous, finally puberulent; floriferous twiglets (3–)6–20 cm. Leaves chartaceous, occasionally anisophyllous; blades elliptic to oblong, obovate or ovate, 5–19 × 1.5–6.5 cm, glabrous, veins subglabrous or glabrous above, subglabrous below; apex acute (to less often rounded) with acumen 5–10(–15) × 5 mm; base cuneate (to sometimes attenuate), sometimes asymmetrical; midrib and secondary veins usually prominulous below; secondary veins (5–)7–11 each side, usually eucamptodromous; hairy pocket or pit domatia in most branch vein angles of midrib and usually along secondary veins, sometimes extending several mm from branch vein angle; nodules scattered on blade; fourth and higher order venation usually slightly more clearly visible above; venation density medium to fine. Stipules cup-shaped, deciduous, subglabrous to puberulent externally, pubescent internally, awn cuspidate, 2 × 0.5 mm. Inflorescences subrotund to corymb-shaped in outline or with subunits of these shapes, (0.5–)1–8 cm across, pubescent to puberulent, sessile, flowers (10–)25–100; sheathing bracts rotund lobed or unlobed and cup-shaped, puberulent externally, pubescent internally, sometimes with linear awns 2–4 mm; other bracts ± ovate, to ca. 3 mm, most larger ones concave with 1–3 fimbriae, or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 1.5–2 mm long, 2–2.3 mm wide halfway up; lobes valvate, oblong, ovate, rotund, long or short triangular (or less often subquadrate or pentagonal), 0.5–2(–2.5) × 1–1.5 (–2) mm, pubescent, usually carinate, rim lighter.

Corolla white, tube cylindrical, 2–6 × 1–2 mm; lobes 5–8 mm. Anthers septate. Style clavate, pubescent, exserted 6–11 mm. Prefruiting ovules 2, ± reniform, attached ca. halfway up septum.

Additional specimens examined. CAMEROON. **South Province:** Bitye, River Dja (fl), *Bates 1573* (BM, MO).

Pavetta cellulosa is known only from Zaïre except for the collection reported here from lowland forest in eastern South Province, south-central Cameroon.

Although the collection from Cameroon differs from ones from Zaïre in having some calyx lobes more elongate and in having domatia less prominent or common along secondary veins, infraspecific taxa are not created here in the absence of more Cameroon material.

The anther thecae of *Pavetta cellulosa* are nearly all septate in open flower after dehiscence. This distinguishing feature otherwise occurs in subgenus *Baconia* only in *P. urophylla* subsp. *urophylla*, which does not occur in Cameroon. Other features of *P. cellulosa* useful for identifying nonflowering specimens are the partly deciduous stipules, which leave behind bases of stipule sheaths that sometimes dry conspicuously lighter brown than the dark brown stem, and the similarity to *P. longibrachiata* and *P. brachysiphon* in leaf morphology. For example, leaves of *P. cellulosa* tend to dry golden brown below, darker brown above, and domatia are usually along lateral veins as well as the midrib. Higher order venation tends to be more obvious above than below, however, unlike in the latter two species, and upper leaf surfaces are not papillate as they usually are in those two species.

8. Pavetta corymbosa (A. P. de Candolle) F. N. Williams, Bull. Herb. Boissier Sér. 2: 378. 1907. *Baconia corymbosa* DC., Ann. Mus. Natl. Hist. Nat. 9: 219. 1807. *Verulamia corymbosa* DC. ex Poir., Encycl. Méth. Bot. 8: 543. 1808. TYPE: Sierra Leone. 1785 (fl), *Smeathman s.n.* (holotype, G-DC not seen; probable isotype, MPU photocopy seen; reported as "Stadman" for *Verulamia corymbosa*).

Pavetta rhombifolia Bremek., Repert. Spec. Nov. Regni Veg. 37: 64. 1934. TYPE: Sierra Leone. Highlands of Bafodya, *Scott Elliot 5506* (K).

KEY TO THE VARIETIES OF *PAVETTA CORYMBOSA* IN CAMEROON

1. Floriferous twiglets glabrous to subglabrous; leaf veins subglabrous to puberulent below; most calyx lobe bases overlapping after flowers open ..... var. *corymbosa*
1. Floriferous twiglets pubescent; leaf veins puberulent to pubescent below; >10% of calyx lobe bases overlapping but most calyx lobes valvate after flowers open ..... var. *neglecta*

a. Pavetta corymbosa var. corymbosa

Pavetta corymbosa var. *glabra* Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 70. 1934.

Shrubs to 3 m. Twiglets glabrous to subglabrous, floriferous twiglets to 25 cm, sometimes strongly curved. Leaves chartaceous to coriaceous, sometimes anisophyllous, blades above and below and veins above glabrous (to less often subglabrous), veins below subglabrous to puberulent; blades elliptic to ovate or obovate, 4–17 × 1–6.5 cm; apex acute (to occasionally obtuse) with acumen 3–8 × 2–4 mm; base cuneate to attenuate, often asymmetrical; midrib prominent below, secondary veins prominulous below, 7–10 each side, sometimes joined 1–6 mm from margin; nodules along midrib and scattered on blade; pubescent domatial tufts, pockets or pits in branch vein angles of midrib and some secondary veins; fourth and higher order venation more obvious below; venation density very fine. Stipules cup-shaped, subglabrous to glabrous outside, pubescent inside, awns linear or cuspidate, ± falcate, 2–5 mm. Inflorescences subrotund to corymb-shaped in outline, 5–7 cm across, pubescent to puberulent, peduncle absent or ca. 2 mm, flowers 50–100; sheathing bracts unlobed and cup-shaped or rotund or pentagonal lobed, puberulent or subglabrous outside, at least sometimes glabrous inside, sometimes with fimbriae to 2 mm or linear awns ca. 2 mm; foliar bracts 7–50 mm usually present; other bracts obovate to ovate or linear, to 3 mm, sometimes with fimbriae 1–2 mm, or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 1.2–1.5 mm long, 2–3 mm wide halfway up, lobe bases usually overlapping, lobes rotund to compressed rotund, subquadrate, obovate or shallowly 2-lobulate, ca. 1–2 × 1.5–2 mm, pubescent to subglabrous, sometimes carinate, rim much lighter. Corolla white; tube cylindrical, 4–8 × 2 mm; lobes 9–11 mm. Style clavate, puberulent, exserted 9–14 mm. Fruits ca. 1 cm across, subglabrous or glabrous. Seeds 2, attached ca. halfway up septum, concave.

Additional specimens examined. SIERRA LEONE. (fl), *Hormont s.n.* (BM left side of sheet). CAMEROON. **Adamaoua Province(?):** Dodéo, Mar. (fl), *Félix 339* (HBG).

b. Pavetta corymbosa var. neglecta Breme-

kamp, Repert. Spec. Nov. Regni Veg. 37: 70. 1934. TYPE: Ghana. Volta Region, formerly Togoland: Kpandu, 1924 (fl bud & fl), *Robertson 102* (holotype, BM; isotype, MO).

Similar to variety *corymbosa* except that the twiglets are pubescent, there is more vestiture on leaf veins above and below, and most calyx lobes are valvate after flowers open.

Other character states of Cameroon representatives of the two varieties overlap to varying degrees (see Manning, 1990, for details). The small number of collections from Cameroon and large number of collections from elsewhere suggest that revision of this species may result in combination of the two varieties or other changes.

Additional specimens examined. CAMEROON. **Northwest Province:** Ndop plain between Bamali and Bambalang, Apr. (fl bud & fl), *Brunt 357* (K); locality uncertain but Northwest Province thought most likely = Metchie River 2 km N of Bamougoum, May (fl bud & fl), *de Wilde & de Wilde-Duyfjes 2519* (BR, P, WAG). **West Province:** Dschang, May (fl bud & fl), *Félix 5204* (P).

Both varieties of *Pavetta corymbosa* occur in savanna and have a more northern distribution than any other species of subgenus *Baconia* except *Pavetta lasioclada*. The presence of variety *corymbosa* very near the Nigerian border with northern Adamaoua Province in Cameroon is part of a distribution west to Sénégambia in the Guineo-Congolian/Sudanian Transition Zone sensu White (1979). The presence of variety *neglecta* in West and Northwest Provinces of Cameroon is part of a distribution at least as far west as Ivory Coast and as far east as Central African Republic (Hepper & Keay, 1963), mainly in the Guineo-Congolian/Sudanian transition zone sensu White (1979), despite the representatives from Cameroon occurring in the Lower Guinean subcentre of specific endemism sensu White (1979).

Pavetta corymbosa var. *neglecta* grows in gallery forest. All plants from Cameroon for which there are field data were collected near water. There are no field data on the Cameroon sheet referred to variety *corymbosa*.

Pavetta corymbosa is most commonly identified by its often overlapping calyx lobe bases, a feature also found in *P. robusta* and a few other species. Leaves are smaller and inflorescences smaller or fewer flowered than in similar species such as *P. robusta* and *P. calothyrsa*. Flowers are larger than in most species from Cameroon.

Although Houttuyn purportedly described another taxon as *Pavetta corymbosa* in 1813 (Hiern, 1877), the name Houttuyn actually gave that taxon was *Crinita capensis* Houtt. Attempts to find a valid publication of *Pavetta corymbosa* Houtt. at BR, K, and elsewhere have been unsuccessful; all references to it I have seen have been as a synonym of later names. Thus, I follow Bremekamp (1934) in treating *P. corymbosa* Houtt. as a nomen nudum. The currently accepted name *Pavetta corymbosa* (DC.) F. N. Williams was thus available when published in 1907 and is thus retained.

9. Pavetta gabonica Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 77. 1934. TYPE: Gabon. Sierra del Crystal: 1°N, July 1862 (fl), *Mann 1729* (holotype, K; isotype, P).

Shrubs to 3 m. Twiglets glabrous or subglabrous, floriferous twiglets (2–)5–35 cm. Leaves chartaceous to subcoriaceous, sometimes anisophyllous; blades obovate to oblong (less often elliptic or ovate), (1.5–)3–25 × (0.5–)1–11 cm; blades and major veins glabrous (or sometimes subglabrous below); apex acute to obtuse (or occasionally rounded), acumen (2–)5–25 × (1–)3–12(–30) mm, rarely absent; base cuneate to attenuate (or occasionally obtuse), sometimes asymmetrical; midrib prominulous below toward base; secondary veins 4–10 each side, sometimes joined 2–5 mm from margin; small tuft, pit, pocket, or intermediate between pocket and pit domatia sometimes in branch vein angles of midrib and rarely along secondary veins; nodules sometimes scattered on blade, less often along midrib; fourth and higher order venation usually more obvious above but also visible below, occasionally equally obvious above and below; venation density medium. Stipules deciduous, unlobed and cup-shaped to triangular lobed, pubescent inside, glabrous or subglabrous outside; cuspidate to linear awn 1–2(–5) mm. Inflorescences rotund to subrotund, irregular (or less often pyramidal) in outline, 1–5.5 cm across, flowers sometimes congested, lower branches and subunits often well spaced, pubescent to puberulent (to rarely glabrous) distally, subglabrous to puberulent (rarely glabrous) proximally, usually with peduncles to 10 mm, sometimes with broadly spreading sheathing bracts along and at bases of peduncles; flowers 10–150; sheathing bracts rotund lobed, partly deciduous, glabrous or subglabrous outside, pubescent to subglabrous inside, sometimes with linear awns ca. 1 mm, occasionally with foliar appendages 3–4 mm; other bracts ± ovate to obovate, to 4 mm, often with 1–many fimbriae to 2 mm, or 1–several fimbriae or a tuft of hairs borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 0.7–1 mm long, 1.2–2 mm wide halfway up; lobes valvate,

deltoid to pentagonal, rotund (or less often subquadrate, subrotund, or truncate), (0.1–)0.2–1 × 0.7–1.5 mm, puberulent to subglabrous, sometimes carinate, rim lighter. Corolla at least sometimes dark glaucous green in bud and cream, yellow, yellowish white, or greenish later, tube usually broadening from base to up to ca. twice as wide at throat, otherwise subcylindrical, 2–4 × (0.5–)1–2 mm; lobes (2–)3–5 mm. Style clavate, pubescent (or less often puberulent), exserted 3–7 mm. Fruits ca. 5–7 mm across, subglabrous or glabrous, orange, brownish, or dull yellow. Mature seeds 2 or 1, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** Kumba = Johann-Albrechtshöhe (fl), *Staudt 565* (S); Bakolle Bakossi on Kumba-Mamfe road, May (fr), *Etuge & Thomas 146* (MO); Bakossi Mountains W of Bangem, Jan. (fl), *Thomas & McLeod 5296* (MO), Jan. (fl & fr), *Thomas & McLeod 5354* (MO); crest of Nta Ali, 30 km SE of Mamfe, June (fr), *Letouzey 13862* (BR, YA). **Centre Province:** 30 km SW of Eséka, Dec. (fl), *de Wilde & de Wilde-Duyfjes 1493B* (BR, P, WAG); 30 km WNW of Eséka, Dec. (fr), *de Wilde & de Wilde-Duyfjes 1493* (BR, MO, P, WAG, YA); near Ngong 25 km NE of Eséka, Dec. (fl bud & fl), *Letouzey 12347* (YA); 90 km W of Yaoundé, Nov. (fr), *de Wilde et al. 3907* (K, WAG); 23 km W of Yaoundé, June (fr), *Manning 2128* (MO), *2134* (MO), *2141* (MO). **Littoral Province (Centre?):** Kéllé River, 50 km NW of Eséka, Nov. (fl bud), *de Wilde & de Wilde-Duyfjes 1318* (K), (fl bud & fl), *1318C* (WAG) [not *1318* or *1318B* (WAG) or *1318C* (P), which are *Pavetta camerounensis*]. **South Province:** Bipindi, month unknown (fl bud & fl), *Zenker 1204* (BM, HBG, MO, S, W, WAG), *2468* (BM, BR), *4744* (BM, BR, HBG, MO, W), Mar. (fl & fr), *Zenker 268* (BR, GH, MO, P, US, WAG), month unknown (fl & fr), *Zenker 1565* (BM, BR, HBG, K, MO, S, W, WAG), month unknown (fr), *Zenker 2618* (BM, BR, HBG, K, P, W), *3164* (K); Lolodorf (fl), *Staudt 8* (S); Ebemvok 55 km W of Ebolowa, Mar. (young fr), *Raynal & Raynal 10437* (P); Efulen (= Efoulan? or Grand Batanga? or Evouma? or Batanga, Gabon?), Mar. (fl & fr), *Bates 451* (K); 7 km N of Kribi, Nov. (fl bud), *Bos 5611* (P). GABON. Environs of Libreville, July (fl bud), *Klaine 1924* (BR), month unknown (fl), *Klaine 2193* (BR); Abanga Chantier C.E.T.A., June (fl bud & fl), *N. Hallé 2207* (P); Gaboon River, 1°N, July (fl bud & fl), *Mann 962* (K).

Pavetta gabonica occurs in Gabon and southwestern Cameroon, centered in the Lower Guinean subcentre of specific endemism sensu White (1979). Within Cameroon, it occurs in western South Province, southwestern Centre Province, and the eastern half of Southwest Province. It is typically a small shrub of shady wet forests, sometimes near watercourses or in swampy areas. Usually a lowland species, it also has been found at elevations of 800–900 m west of Yaoundé and similar elevations in mountains of northern Southwest Province.

Pavetta gabonica has two features rather unusual in subgenus *Baconia*: orange to yellow or brownish fruits and often yellowish flowers. It is compared with *P. brachycalyx* following the description of that species. *Pavetta brachycalyx* appears to be a close montane relative of the more widespread *P. gabonica*.

The type specimen from Gabon is smaller leaved and fewer flowered than most members of the species, especially those in Cameroon. Other collections from Gabon bridge the morphological gap between the type and Cameroon representatives.

10. Pavetta grossissima S. D. Manning, sp. nov. TYPE: Cameroon. Southwest Province: 5 km NE of Mundemba, Nov. 1986 (fr), *Manning 944* (holotype, MO; isotypes, BR, K, YA). Figure 11.

Frutices. Folia nervis secundariis utroque 5–12; reticulo grossissimo. Infructescentiae suburbellatae, puberulae, 0.1–2 cm latae. Lobi calycini in fructu valvati, rotundati, rotundato-compressi, ovati vel pentagonales, ca. 0.2–1 × 1 mm. Fructus maturi interdum cum calyce persistenti, aurantici.

Shrubs to 1 m. Twiglets puberulent (to sometimes subglabrous), floriferous twiglets 4–20 cm and probably longer (less often absent or <4 cm). Leaves chartaceous, sometimes anisophyllous; blades oblong to elliptic, obovate (or uncommonly ovate), 4–22 × 2–9 cm, glabrous; veins puberulent to subglabrous; apex acute or rounded, subacuminate or with acumen 5–20 × 2–11 mm; base cuneate to obtuse (occasionally rounded), sometimes asymmetrical; midrib and secondary veins prominulous below, secondary veins 5–12 each side, mostly eucamptodromous; minute tuft domatia sometimes in branch vein angles of midrib, sometimes accompanied by pits; nodules scattered on blade, sometimes along midrib; third and higher order venation obvious above and below; venation density very coarse. Stipules deciduous, rotund lobed to unlobed and cup-shaped, subglabrous to puberulent externally, glabrous internally; awn linear, 2 mm to cuspidate, 4 × 2 mm. Infructescences subumbellate, rotund in outline or reduced and of irregular shape, 0.1–2 cm across, puberulent, peduncle to 5 mm or absent; fruits 1–12; sheathing bracts rotund lobed to unlobed and saucer-shaped, puberulent externally, glabrous or subglabrous internally, awns deciduous, fimbriae if present ca. 0.5 mm; other bracts ± obovate to linear or subquadrate, ca. 1 mm, fimbriae if present 0.5–1 mm; bracteoles resembling smaller bracts. Calyx seen only on fruits, tube then 0.5–1 mm long, 1–2 mm wide halfway up; lobes then valvate, ± rotund, compressed rotund, ovate or pentagonal, 0.2–1 × 1

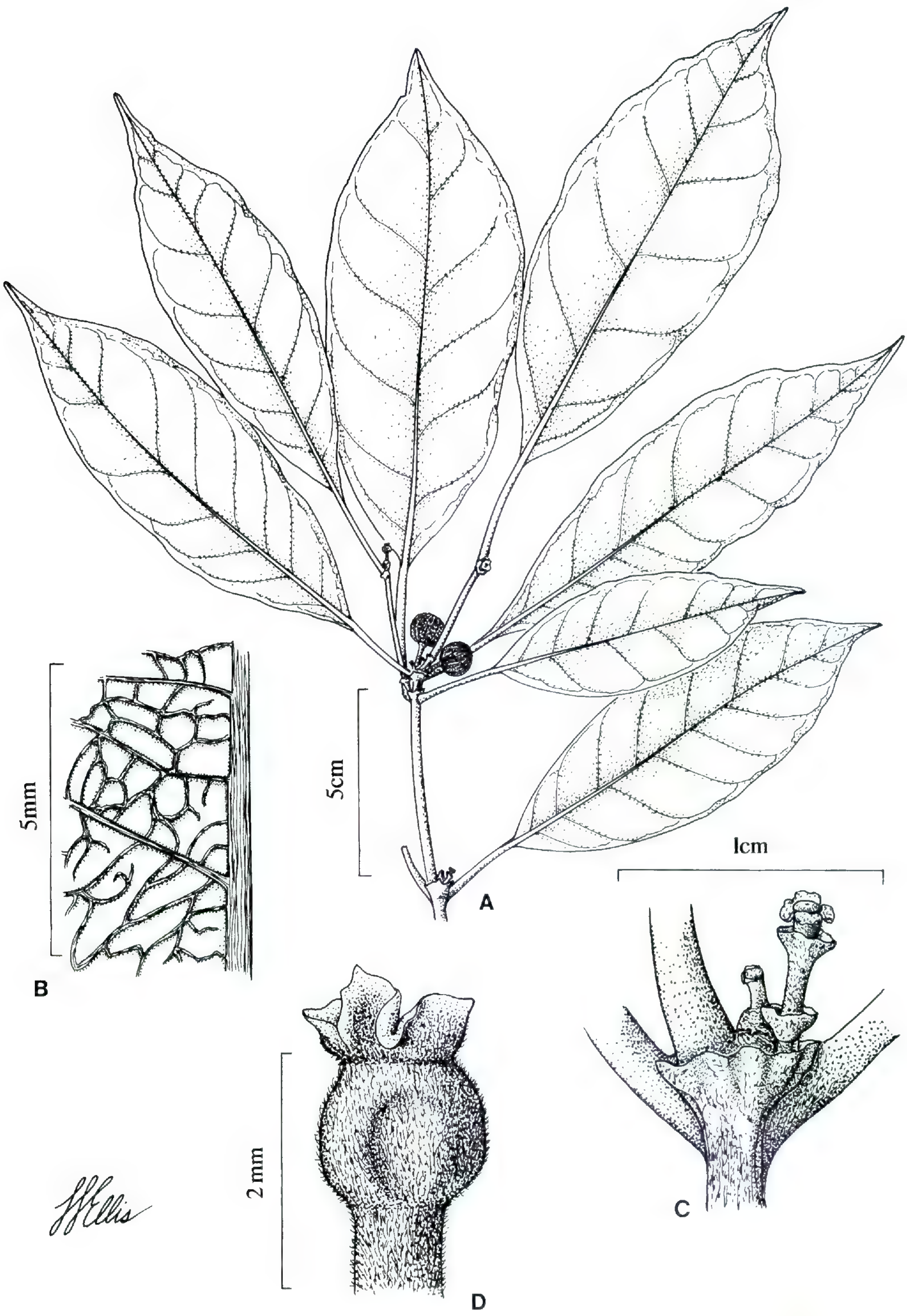


Figure 11. *Pavetta grossissima* (*Manning 944*, MO).—A. Habit, including terminal and axillary infructescences.—B. Details of leaf venation, coarsest seen in subgenus *Baconia*.—C. Axillary infructescence. D. Young fruit with persistent calyx.

mm, puberulent, sometimes carinate, rim lighter. Other floral parts not seen. Fruits ca. 1 cm across, glabrous or subglabrous, sometimes with persistent calyx, orange. Mature seeds 2, or 1 and empty second locule then very reduced, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** 10 km SE of Mundemba, Nov. (fr), *Manning 970* (MO), *973* (BR, K, MO); 5 km NE of Mundemba, Nov. (fr), *Manning 906* (MO), *929* (MO); Korup National Park, Apr. (young fr), *Manning 1710* (MO), *1722* (MO), *1767* (MO), Dec. (fr), *Thomas 4111* (MO), June (vegetative), *Thomas 449* (BR).

Pavetta grossissima is known only from in and near Korup National Park in far southwestern Southwest Province, Cameroon. It is a small shrub of extremely wet forest understory in fully and partly shaded areas at elevations of 120 m or less.

Pavetta grossissima is distinguished principally in having the coarsest reticulation of higher order leaf veins of all species of subgenus *Baconia*. It is so named because of this. Also, orange fruits are known otherwise only in *P. gabonica*, which does not have leaf vein reticulation as coarse or inflorescences as condensed as *P. grossissima*.

11. Pavetta hookeriana Hiern, Fl. Trop. Africa 3: 176. 1877. *Baconia montana* Hook. f., J. Proc. Linn. Soc., Bot. 7: 196. 1864. *Ixora hookeriana* (Hiern) Kuntze, Revis. Gen. Pl. 1: 287. 1891. TYPE: Cameroon. Southwest Province: Mt. Cameroon, ca. 2100 m, Dec. 1862 (fl & fr), *Mann 2166* (holotype, K).

Pavetta exellii Bremek., Repert. Spec. Nov. Regni Veg. 37: 73. 1934. TYPE: Equatorial Guinea. Bioko Island, Jan. 1933 (fl), *Exell 787* (holotype, BM).

KEY TO THE VARIETIES OF *PAVETTA HOOKERIANA* IN CAMEROON

1. Leaf veins glabrous, subglabrous, or rarely puberulent but not intermittently pubescent below ..... var. *hookeriana*
1. Leaf veins intermittently pubescent below (Fig. 12) ..... var. *pubinervata*

a. **Pavetta hookeriana** var. **hookeriana**

Shrubs or small trees to 10 m. Twiglets glabrous (or subglabrous in some plants from the Oku area), floriferous twiglets 3–21 cm. Leaves coriaceous or subcoriaceous, sometimes anisophyllous; blades glabrous, obovate to elliptical, 1.5–14.5 × 0.7–7 cm, veins glabrous to subglabrous or rarely puberulent above or below, apex acute to obtuse (less often rounded), acumen if present usually subequal in length and width, 1–9 × 1–9 mm; base cuneate (to sometimes attenuate), sometimes asymmetrical; midrib and secondary veins sometimes prominulous below, secondary veins (3–)5–14 each side, occasionally joined 2–10 mm from margin, otherwise eucamptodromous; pubescent tuft, crypt, pocket or pit domatia sometimes in branch vein angles of midrib and rarely of secondary veins, sometimes elongated several mm above branch vein angle; nodules absent to fairly numerous, most elongate and close to midrib; fourth and higher order venation seldom clearly visible, usually more visible below than above; venation density fine. Stipules cup-shaped, pubescent internally, glabrous (or at times subglabrous) externally, awn deciduous, linear to cuspidate, 1.5–5 mm. Inflorescences rotund to corymb-shaped in outline or with subunits of these shapes, 0.5–8 cm across, puberulent to glabrous, sessile, flowers 10–85(–150); sheathing bracts rectangular lobed to unlobed, then cup-(or less often saucer-)shaped, pubescent inside, glabrous to subglabrous outside, sometimes with fimbriae to 1.5 mm, linear awns 1–4 mm or foliar appendages 5–15 mm; foliar bracts if present 1–5 cm long or resembling slightly reduced foliage leaves; other bracts absent or linear to ovate or quarter-spherical, to ca. 3 mm, with or without 1–several fimbriae to 2 mm, or a fimbria or tuft of hairs borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 1–1.5 mm long, 1.5–2.5 mm wide halfway up; lobes valvate, rotund (or less often oblong, ovate, triangular, or pentagonal), 0.7–1.5(–3) × 1–2 mm, puberulent or subglabrous, sometimes carinate, often reflexed when dry, rim lighter. Corolla white or cream, tube sometimes green or lobes green tipped outside; tube usually cylindrical, 2–5 × 1–2(–4) mm; lobes 4–8 mm. Style clavate, puberulent or subglabrous, exserted 4–8 mm. Stigma sometimes conspicuously 2-lobed. Fruits ca. 8–10 mm across, glabrous or subglabrous, bluish green, later black. Mature seeds 1 or 2 (except one empty fruit seen), attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** Mt. Cameroon (fl bud), *Maitland 992* (B), (fl bud, fl & fr), *Maitland = TDM 1312* (B, K), Mar. (fl), *Boughey GC 7005* (K), *Deistel 77* (GH), *Onochie 9525* (BM, BR, P, identified also as *Brenan 9525*), *Swarbrick 2326* (YA), Apr. (fl), *Morton GC 6840* (K), *Thomas 4608* (MO); around crater of Manéngouba, Feb. (fl bud), *Thomas 3145* (MO). **West Province:** Dschang, Mt. Bamboutos, June (fr), *Saxer 97a, 97b* (K); Djuttitsa, Bamboutos, Nov. (vegetative), *Meurillon 496* (HBG), May (fr), *Meurillon 1281* (K); Babadjou, Mt. Santa, Dec. (fl bud, fl & fr), *Félix 2792* (HBG, K, P). **Northwest Province:** Santa, Mt. Santa, June (fr), *Saxer 12* (K); Bafut-Ngemba Forest Reserve near nursery, Apr. (fl bud), *Ujor FHI 30050* (K); Bafut-Ngemba Forest Reserve, NW face of

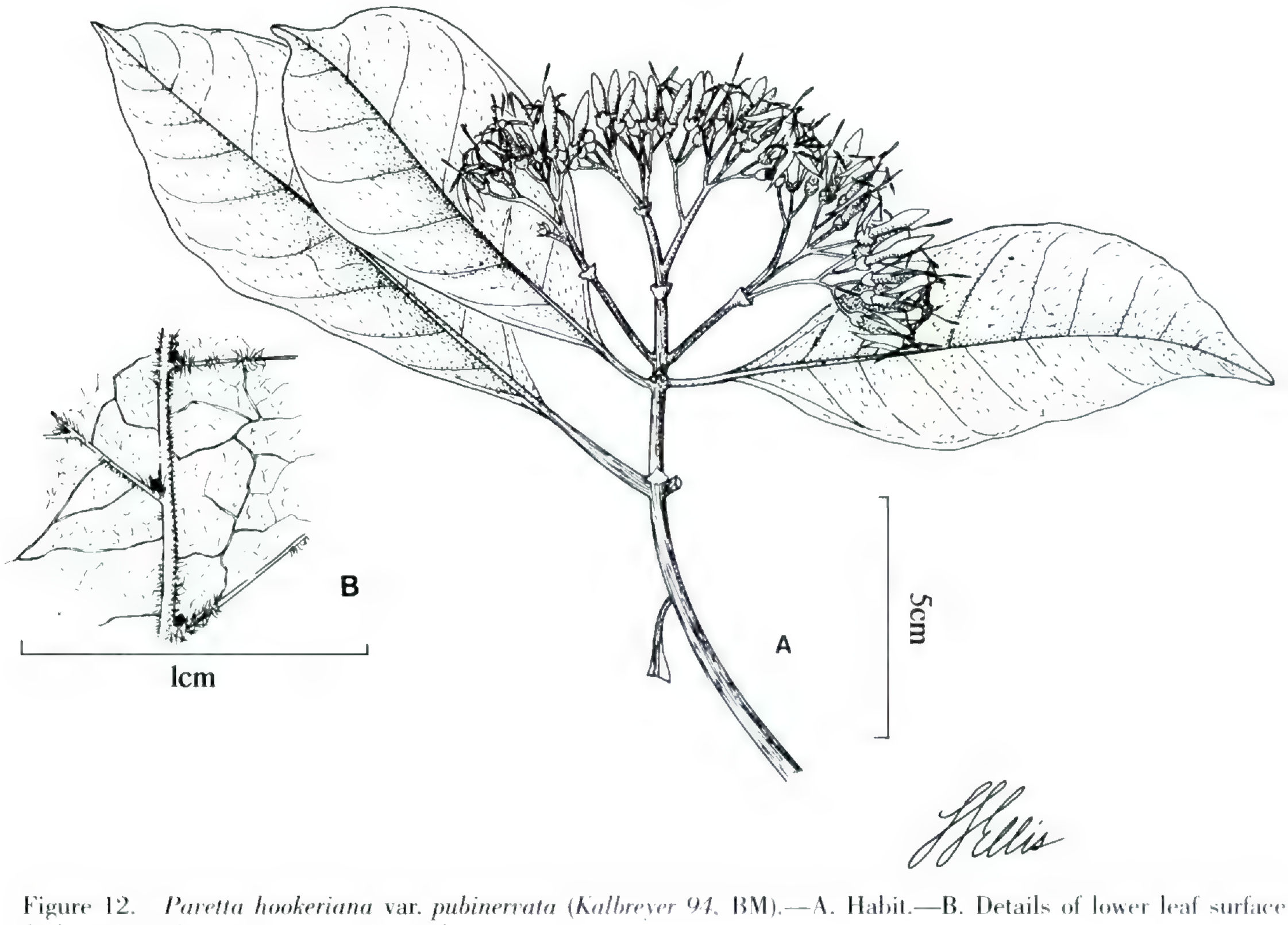


Figure 12. *Pavetta hookeriana* var. *pubinervata* (*Kalbreyer 94*, BM).—A. Habit.—B. Details of lower leaf surface with domatia and intermittent vestiture along veins.

Mbakakeka Mt., Feb. (fl), *Hepper 2160* (BR); Bafut-Ngemba Forest Reserve, road to Lake Bambuluwe, Mar. (fl), *Onochie FHI 34850* (K); Bafut-Ngemba Forest Reserve, foot path between Menda Nkwe and Awing, July (fr), *Manning 2177* (MO); 40 km NE of Bamenda, path from Acha Abaw to Lake Oku, Dec. (fl bud, fl & fr), *Letouzey 13448* (BR, YA); Oku area, June (fl), *Brunt 607* (K), Aug. (fl), *C.N.A.D. 1805* (P), July (fl), *Letouzey 8937* (P), Feb. (fl), *Thomas 4386* (MO), Apr. (fl), *Thomas & McLeod 6006* (MO).

b. Pavetta hookeriana var. **pubinervata** S. D. Manning, var. nov. TYPE: Cameroon. Southwest Province: Buea or Limbe, Mar. 1877 (fl), *Kalbreyer 94* (holotype, K, labeled "Cam. Victoria"; isotype, BM, labeled "Cam. Bonjango" = part of Buea, top of sheet only). Figure 12.

A varietate *hookeriana* foliis nervis subter interrupte pubescentibus differt.

Similar to variety *hookeriana* except leaf veins intermittently pubescent below.

Pavetta hookeriana var. *pubinervata* has larger leaves than most specimens of variety *hookeriana*, which usually has small leaves and light bark and often has many short internodes. Other features of variety *pubinervata* include some leaf blades ovate, some leaves with a few hairs above and below, fourth and higher order venation easily visible below, sheathing bracts sometimes deltoid lobed, pedunele absent or ca. 4 mm, calyx tube occasionally only 0.7 mm long or 1.2 mm wide halfway up, and calyx lobes occasionally as short as 0.5 mm.

Variety *pubinervata* is given varietal status mainly because of the sharp difference in leaf vestiture from any of the numerous collections of variety *hookeriana*; it is also geographically distinct.

Pavetta hookeriana is a montane species occurring at elevations of 1500–2800 m (var. *hookeriana*) or 500 m (var. *pubinervata*) in or at edges of forest. It is the only widespread high elevation species of subgenus *Baconia* in Cameroon. It occurs only on volcanoes, including Mt. Cameroon, Mt. Oku, and other mountains in Cameroon and the offshore islands Pagalu and Bioko of Equatorial Guinea. In Cameroon, this distribution includes locations in eastern Southwest Province, western West Province, and southern and central Northwest Province. Variety *pubinervata*, known only from the type, was collected on Mt. Cameroon.

Nodules are often more numerous on plants of this species from more northern locations than from elsewhere.

Some larger-leaved specimens of variety *hookeriana* (e.g., *Deistel 77* and *Onochie FHI 34850*)

look similar to *P. molundensis*, a species of lower elevations occurring further east. However, *P. molundensis* has more flowers per inflorescence, longer calyx lobes, and larger leaves. *Pavetta hookeriana* also superficially resembles high altitude specimens of *P. kupensis* but has much shorter styles and usually rotund to ovate, often reflexed calyx lobes longer than the usually somewhat compressed (Fig. 5) ones of *P. kupensis*.

Kalbreyer 94, the only specimen of variety *pubinervata*, is probably the same specimen referred to *Pavetta owariensis* as "*Kalbreyer 92*" by Hepper and Keay (1963) and referred to *Pavetta intermedia* Bremekamp as "*Kalkbreyer 92*" by Bremekamp (1934). The handwritten numeral interpreted as a "4" here, though ambiguous, is clearly different from a "2" in the same handwriting later on the same sheets.

12. Pavetta kribiensis S. D. Manning, sp. nov. TYPE: Cameroon. South Province: 25 km ENE of Campo, Mar. 1968 (fl bud & fl), *Letouzey 9148* (holotype, P; isotypes, BR, YA). Figure 13.

Frutices. Rami glabri. Folia glabra, nervis secundariis utroque 5–12. Inflorescentiae in ambitu rotundatae ad subcorymbosas, 0.5–2 cm latae, congestae, glabrae. Lobi calycini valvati (vel aliquando parum superpositi basi), rotundati, (vel interdum pentagonales, rotundato-compressi vel deltoidei), 0.2–1 × 0.7–1.5 mm. Corolla tubo 4–6 mm, lobis 4–7 mm, lobis interdum super tenuiter prope faucem puberulis.

Shrubs to 1 m. Twiglets glabrous, floriferous twiglets 1–19.5 cm. Leaves chartaceous or thinly subcoriaceous, glabrous, sometimes anisophyllous; blades oblong, obovate, elliptical (or less often ovate), 2.5–21.5 × 1–7.5 cm; apex obtuse to acute or rounded, often asymmetrical, acuminate, acumen usually abrupt, 1–27 × 1–9 mm; base attenuate to cuneate, sometimes asymmetrical; midrib and secondary veins often prominulous below especially toward base, secondary veins sometimes impressed above, 5–12 each side, sometimes joined 1–7 mm from margin; domatia, if present, usually pubescent pockets or tufts in most branch vein angles of midrib; nodules scattered on blade, rarely on midrib; fourth and higher order venation usually more obvious below; venation density medium. Stipules deltoid to rotund, pentagonal or attenuate lobed or truncate, glabrous; awn sometimes deciduous, cuspidate to linear, to ca. 10 mm. Inflorescences subumbellate, rotund to subcorymb-shaped in outline, 0.5–2 cm across, congested, glabrous, peduncle absent or to 10 mm; flowers (1–)5–40; sheathing bracts unlobed and cup- or bowl-shaped, truncate, or rotund, ovate or narrowly triangularly lobed, glabrous externally and internally, linear awns if present to 4 mm, foliar appendages 2–6 mm; foliar bracts if present resembling foliage leaves, sometimes reduced proportionately more in length than width; other bracts often obscured by sheathing bracts in congested inflorescences, ± ovate, 1–2 mm, without fimbriae but sometimes with a ± oblong, blunt pointed awn ca. 1 mm; bracteoles resembling smaller bracts or absent. Calyx tube 1–1.3 mm long, 1.5–2.5 mm wide halfway up; lobes valvate (or bases at times slightly overlapping), rotund (or less often pentagonal, compressed rotund (Fig. 5) or deltoid), 0.2–1 × 0.7–1.5 mm, glabrous, sometimes carinate, rim usually lighter. Corolla white or creamy white; tube usually broadened from base to apex, 4–6 × 1–3 mm; lobes 4–7 mm, sometimes thinly puberulent above near base. Style narrowly clavate to fusiform, puberulent to pubescent, exserted 4–8 mm. Young fruits dark green, ca. 9 mm across, glabrous, with persistent calyces. Seeds 2, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **South Province:** 15–25 km SW of Zingui = ca. 45 km SSE of Kribi, Mar. (fl bud & fl), *Letouzey 9116* (BR, P); 12 km ENE of Kribi, Lolodorf road, May (fr), *Bos 4638* (WAG); 19 km ENE of Kribi, Lolodorf road, Mar. (fl), *Bos 4137* (WAG); 40 km ENE of Kribi, Lolodorf road, Jan. (fl), *Bos 6202* (WAG).

Pavetta kribiensis is endemic to western South Province, Cameroon. It occurs in wet forest, sometimes along streams.

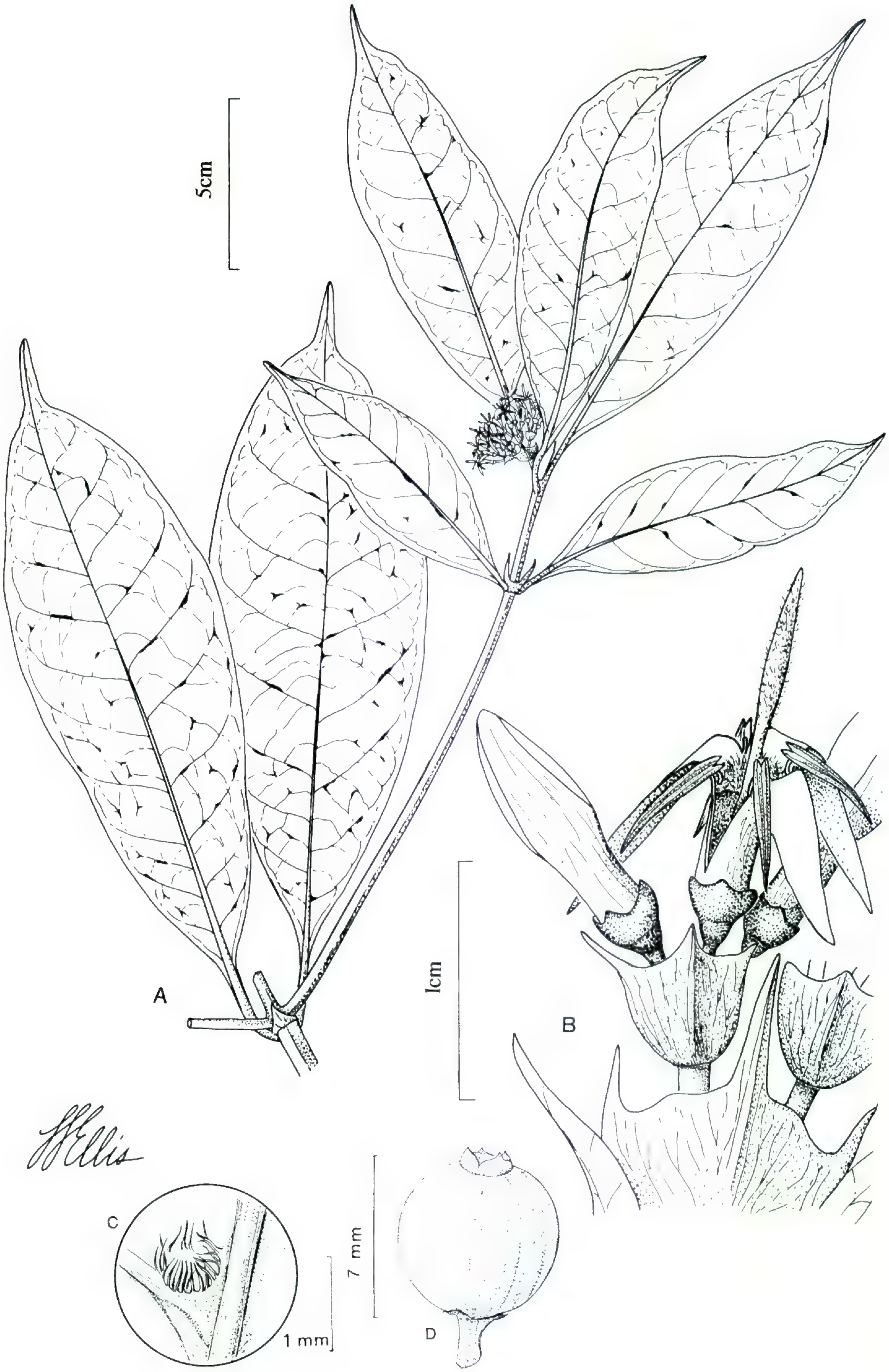
The distal, nonsheathing bracts of *Pavetta kribiensis* are unusual in sometimes having a more or less oblong, blunt-pointed awn rather than the thin fimbriae found in most species.

Pavetta kribiensis resembles *P. staudtii* vegetatively and in nodule patterns. It is distinct from *P. staudtii* in having rotund to deltoid calyx lobes rather than usually subquadrate (Fig. 5) ones, as well as in its more condensed inflorescences and nonfimbriate bracts.

13. Pavetta kupensis S. D. Manning, sp. nov. TYPE: Cameroon. Southwest Province: W side

→

Figure 13. *Pavetta kribiensis* (A, B, *Letouzey 9148*, P; C,D, *Bos 4638*, WAG).—A. Habit including bacterial nodules.—B. Part of inflorescence with open flower, bracts covering inflorescence branches for most of their lengths, awns on bracts.—C. Domatium on lower leaf surface.—D. Fruit.


5cm
A
lcm
B
C
1 mm
7 mm
D

of Mt. Kupe, Feb. 1986 (fl), *Thomas & McLeod 5481* (holotype, MO; isotypes, BR, K, P, WAG not seen, YA not seen). Figure 14.

Frutices. Folia laminis glabris, valde obovatis vel oblanceolatis (ad interdum ellipticas vel oblongas), apice obtuso ad rotundatum; nervis secundariis utroque 5–9; domatiis foveis vel cryptis interdum puberulis secus costam et interdum in angulis externis nervorum secundariorum et aliorum nervorum secundariorum vel tertiariorum (vel raro nullis); venulis utrinque obscuris. Inflorescentiae in ambitu subrotundatae ad corymbosas vel in monades subrotundatae ad corymbosas divisae, 2–9 cm latae. Lobi calycini valvati, triangularo-compressi ad rotundato-compressos (ad aliquando rotundatos vel non profunde 2-lobulatos), 0.1–1 × 1–2 mm, glabri ad subglabros. Corolla tubo (4–)6–8 mm longo, lobis 8–12 mm longis. Styli exserti 11–20 mm.

Shrubs to 4 m. Twiglets glabrous, floriferous twiglets 2–11 cm. Leaves coriaceous, glabrous, sometimes anisophyllous; blades strongly obovate or oblanceolate (to less often elliptical or oblong), 3–19 × 1–7.5 cm; apex obtuse to rounded, usually with acumen 3–10 × 2–8 mm; base cuneate to attenuate, often slightly asymmetrical; midrib prominulous below toward base; secondary veins 5–9 each side, joined 1–10 mm from margin, their connections often conspicuous to the naked eye; domatia usually crypts or pits along midrib and sometimes in external angles of branching secondary veins, sometimes puberulent; nodules few, scattered on blade and sometimes on midrib; fourth and higher order venation obscure, sometimes slightly more obvious above; venation density fine. Stipules deciduous, rotund lobed to unlobed and then saucer- or cup-shaped, pubescent internally, glabrous externally, with cuspidate, falcate awn ca. 1–3 × 1 mm. Inflorescences subrotund to corymb-shaped in outline or with subunits of these shapes, 2–9 cm across, glabrous or subglabrous, sessile, flowers 25–75; sheathing bracts triangular, rotund or compressed rotund lobed to unlobed and then saucer- or cup-shaped, pubescent internally, glabrous externally, with triangular, ovate, or linear awns 1–3 × 0.5–1 mm; other bracts linear, broadly ovate, obovate, or triangular, occasionally carinate, to 3 mm, sometimes with 1–several fimbriae 0.5–2 mm or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 1–1.5 mm long, 2–2.5 mm wide halfway up; lobes valvate, short triangular to compressed rotund (or less often rotund), occasionally shallowly 2-lobulate, 0.1–1 × 1–2 mm, glabrous or subglabrous, sometimes carinate, rim not or narrowly lighter; corolla in bud greenish or white with green vertical stripes, in open flower greenish white; tube cylindrical or subcylindrical, (4–)6–8 × 1–2 mm; lobes 8–12 mm. Style narrowly clavate, puberulent, exserted 11–20 mm.

Additional specimens examined. CAMEROON. **Southwest Province:** between summits of Mt. Kupe, Nov. (fl bud), *Letouzey 450* (BR); Mungo River valley near Konye, 40 km N of Kumba, Dec. (fl bud), *Thomas & Nemba 5197* (MO).

Pavetta kupensis is endemic to Cameroon. It has been found only in forest on and approximately 30 km west of Mt. Kupe in eastern Southwest Province, at elevations from 300 to 2000 m. The lowland specimen has larger leaves than other collections.

The chief distinguishing features of *Pavetta kupensis* are that most leaves are usually strongly obovate and brochidodromous with apices never acute. Styles are exserted farther than in most species, but not as far as in *P. longistyla* S. D. Manning, which also has much longer calyx lobes and larger inflorescences than *P. kupensis* and lacks domatia. Comparisons to other species follow the descriptions of *P. brachycalyx* and *P. hookeriana.*

Collection of more material may reveal intermediates sufficient to combine *Pavetta kupensis* with one or more of its congeners. It is not obviously closer to any one of them than the others.

14. Pavetta lasioclada (K. Krause) Mildbraed ex Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 62. 1934. *Chomelia lasioclada* K. Krause, Bot. Jahrb. Syst. 34: 136. 1909. TYPE: Togo. Sokode, 1904, *Kersting A56* (holotype, B destroyed). LECTOTYPE: Sierra Leone. Falaba, Mar. 1892 (fl bud), *Scott Elliot 5142* (lectotype, selected here, K; isolectotype, BM).

Pavetta baconia Hiern var. *hispida* Scott Elliot, J. Linn. Soc., Bot. 30: 83. 1895. TYPE: Sierra Leone. Near Falaba, Mar. 1892 (fl bud), *Scott Elliot 5412* (= *5142*, K, BM?).

Pavetta ledermannii K. Krause, Bot. Jahrb. Syst. 40: 419. 1913. TYPE: Cameroon. Adamaoua Province, probably: Pass Tchape, Mar. 1909 (fl), *Ledermann 2835* (B destroyed).

Pavetta viburnoides A. Chev., Explor. Bot. Afrique Occid. Franç. 1: 334. 1920. No holotype designated; specimens cited include one from French Sudan (1899) and eight from French Guinea (all 1905).

Pavetta tisserantii Bremek., Repert. Spec. Nov. Regni Veg. 37: 63. 1934. Syn. nov. TYPE: Central African Republic. Balaougu, 17 km N of Bambari, Mar. 1925 (fl), *Tisserant 1865* (P).

Shrubs or small trees to 5(–10) m. Twiglets pubescent especially finally, floriferous twiglets 6.5–26 cm. Leaves chartaceous (to less often coriaceous), sometimes anisophyllous; blades obovate to elliptic or ovate, 4.5–25 × 2–11 cm, pubescent

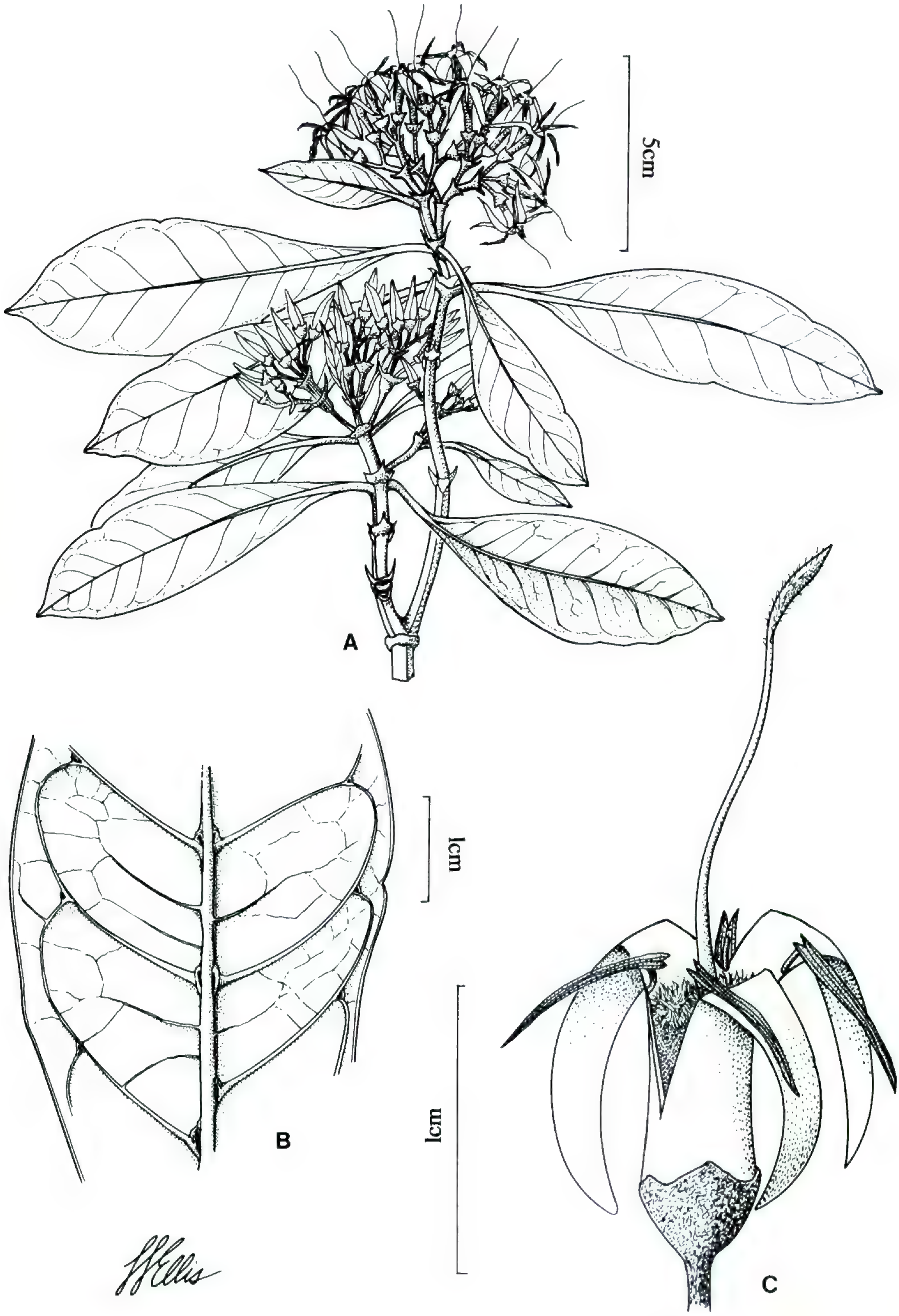


Figure 14. *Pavetta kupensis* (*Thomas & McLeod 5481*, MO).—A. Habit.—B. Details of lower leaf surface with conspicuous submarginal veins, obscure higher order venation, and domatia.—C. Flower.

below, less densely pubescent to subglabrous above, veins pubescent below, pubescent to puberulent above; apex acute to obtuse or rounded, acumen 2–15 × 2–13 mm (or less often absent); base cuneate to obtuse (or less often rounded or truncate), sometimes asymmetrical; midrib and secondary veins prominent or prominulous below, secondary veins 7–15 each side, sometimes joined 1–8 mm from margin; pocket domatia sometimes or tuft domatia rarely present in branch vein angles of midrib (or occasionally other veins); nodules uncommon, along midrib or scattered on blade; some tertiary veins prominent or prominulous below; fourth and higher order venation invisible to obvious; venation density medium to fine. Stipules cup-shaped, pubescent externally, glabrous or subglabrous internally; awn falcate or linear, 2–10 mm. Inflorescences rotund to pyramidal, subpyramidal or corymb-shaped in outline or with subunits of these shapes, 3–17 cm across, lax to congested, pubescent, peduncle absent or ca. 2 mm; flowers 20–200, fragrant; sheathing bracts rotund lobed or unlobed and cup- to saucer-shaped, pubescent externally, subglabrous internally, linear awns 2–7 mm, foliar appendages 7 mm; foliar bracts 1.5–5 cm or resembling slightly reduced foliage leaves, sometimes proportionally broader compared to length than foliage leaves; other bracts semicircular to ovate or deltoid, to ca. 5 mm, sometimes with fimbria ca. 2 mm or fimbriae borne from axis directly; bracteoles resembling reduced bracts sometimes present. Calyx tube 1–1.3 mm long, 2–2.3 mm wide halfway up; lobes valvate, long triangular or pentagonal to ovate, oblong or obovate, 1.5–4 × 1–2 mm, pubescent, not or slightly carinate, rim lighter. Corolla in bud white with green apex or grayish green, in open flower white sometimes quickly becoming rust; tube slightly broadened from base to apex, 4–7 × 1–2 mm; lobes 6–11 mm. Style clavate, puberulent to subglabrous, exserted 7–17 mm. Stigma sometimes 2-lobed, lobes to 1 mm. Ovules 4 in 2 locules with 2 ovules attached to a placenta ca. halfway up on each side of septum, or only 2 or 3 ovules developed. Fruits ca. 8 mm across, thinly pubescent or puberulent, green, pale green, whitish green, or glaucous green becoming brown or bluish black. Seeds 4 with 2 attached to a placenta ca. halfway up on each side of septum, or only 2 or 3 developed, concave.

Additional specimens examined. CAMEROON. **North Province:** Sokorta Manga, 40 km ENE of Bélel, Mar. (fl bud), *Fotius 3191* (YA). **Adamaoua Province:** 8 km S of Ngaoundéré, Oct. (fr), *Breteler 600* (BR, GH, P, WAG, YA); 17 km S of Meiganga, Nov. (fr), *de Wilde et al. 3953* (WAG); Mama, 40 km SE of Meiganga, Oct. (fr), *Letouzey 6104* (BR, YA); Boubala road, Tibati area, Dec. (fl bud & fr), *Letouzey 2551* (BR, YA). **Centre Province:** 15 km W of Méting, Matsari-Linté road, May (young fr), *Biholong 545* (P). **East Province:** 17 km E of Deng Deng, Jan. (fl), *Breteler 998* = *Letouzey 3328* (same collection) (BR, K, WAG, YA). CENTRAL AFRICAN REPUBLIC. Buala, labeled "Kamerun," 6°25′N, 15°30′E, June (young fr), *Mildbraed 9559* (K); Bosum Namgebiet, probably = Bozoum, labeled "Neu-Kamerun," Mar. (fl bud & fl), *Tessmann 2247* (K); Balaougu, 17 km N of Bambari, Mar. (fl), *Tisserant 1865* (P).

Of the species of subgenus *Baconia*, *Pavetta lasioclada* and *P. corymbosa* have the most northern and widest distributions. *Pavetta lasioclada* occurs west at least to Sierra Leone and east at least to Central African Republic in the Guineo-Congolian/Sudanian transition zone sensu White (1979). Most collections from Cameroon have been in Adamaoua Province, others in the southeastern corner of North Province and northern Centre and East Provinces. It occurs in gallery and young forest and forest borders in predominantly savanna areas. The North Province collection is the single known representative of subgenus *Baconia* from either North Province or Far North Province. *Pavetta lasioclada* has been reported from 650 to 1500 m elevations in Cameroon. Bozoum, presently in Central African Republic, was in "Neu-Kamerun" when *Tessmann 2247* was collected in 1914 (U.S. Office of Geography, 1962; Ade Ajayi & Crowder, 1985: Chapters 59 and 62, maps).

The most distinctive feature of *Pavetta lasioclada* is that its fruits often bear two seeds per locule. Other aids to recognition are that the midrib and secondary veins are usually impressed above and prominent below; tertiary veins are often prominent below, sometimes even more so than in *P. tenuissima* and *P. muiriana* S. D. Manning; plants are pubescent to puberulent on most parts, though stipules and sheathing bracts are glabrous or subglabrous inside; and inflorescences are large and flowers fragrant.

Pavetta lasioclada and *P. tisserantii* are here combined because the three differences used to separate them (degree of vestiture on lower side of leaves, number of secondary veins, and number of internodes of flowering shoots) are not reliable. Duplicates or single sheets of some individual collections (e.g., *Breteler 998* = *Letouzey 3328* and *Tessmann 2247*) show much of the range of variation encompassing both former species.

Scott Elliot's description of *Pavetta lasioclada* as *P. baconia* var. *hispida* is the earliest for the species. This was, however, 18 years after the first description of *P. baconia* by Hiern, including five varieties. None of the earlier varieties of *P. baconia*

belongs to *P. lasioclada*. Thus, *P. baconia* is not the correct name for this species. The specific epithet "*lasioclada*" (Krause, 1909) was the next attributed to this species after "*Pavetta baconia* var. *hispida*."

The lectotype chosen here was seen by Bremekamp (1934) along with the later destroyed holotype when he transferred this species from *Chomelia* to *Pavetta*. It is probably also the specimen Scott Elliot used in his original brief description, though he cited it as *5412* rather than *5142*—the locality and description fit.

15. Pavetta laxa S. D. Manning, sp. nov. TYPE: Cameroon. South Province: near Mékomo, 8 km SW of the confluence of Rivers Dja and Lobo, Mar. 1962 (fl bud & fl), *Letouzey 4581* (holotype, YA; isotype, P). Figure 15.

Frutex. Folia laminis super papillatis vel puberulis, subter glabris, nervis utrinque puberulis; apice acuto ad rotundatum; nervis secundariis utroque 6–14; nodulis rarissimis in laminis vel nullis. Inflorescentiae corymbosae vel in monades corymbosas divisae, 3–4 cm latae, laxae. Lobi calycini rotundati (ad interdum oblongos, obovatos vel ovatos apice rotundato), 1–1.5(–2) × 1 mm, pubescentes. Corolla tubo 2–3 mm, lobis 3 mm. Styli exserti 2–4 mm.

Shrubs ca. 5 m. Twiglets puberulent to subglabrous, floriferous twiglets 19–20 cm. Leaves chartaceous, blades papillate or minutely puberulent above, glabrous below, major veins puberulent or subglabrous above and below, top pair of leaves strongly anisophyllous; blades elliptical to obovate (or less often ovate, oblong, or rotund) or reduced to a vestige at the top node, 6–15.5 × 4.5–6.5 cm, often asymmetrical; apex acute to rounded with acumen 7–13 × 4–8 mm; base attenuate (to less often cuneate, cordate, or rounded); midrib and secondary veins prominulous below, secondary veins 6–14 each side, sometimes joined 1–5 mm from margin; domatial tufts of hair occasionally accompanied by pits in branch vein angles of midrib and secondary veins; nodules absent or on blade, very rare; fourth and higher order venation more obvious below than above; venation density medium to fine. Stipules sometimes deciduous, cup-shaped, pubescent internally, subglabrous externally, awn cuspidate, ca. 1–3 × 1 mm, falcate. Inflorescences corymb-shaped or with corymb-shaped subunits, 3–4 cm across, lax, pubescent to puberulent, sessile, flowers ca. 35; sheathing bracts unlobed and cup- to saucer-shaped or ovate lobed, short pubescent, awns ± linear, 0.5–1.5 mm; other bracts ovate, to 2 mm with 1–several fimbriae to 0.5 mm; bracteoles uncommon, resembling bract fimbriae borne from pedicel directly. Calyx tube 0.7–1 mm long, 1.2–1.8 mm wide halfway up; lobes valvate, rotund (or less often oblong, obovate, or ovate with obtuse apex), ca. 1–1.5(–2) × 1 mm, short pubescent, sometimes carinate, rim lighter. Corolla white; tube cylindrical or subcylindrical, 2–3 × 1 mm; lobes 3 mm. Style clavate, pubescent to subglabrous, exserted 2–4 mm. Stigma with 2 connivent lobes.

Pavetta laxa is known only from the type from South Province, south-central Cameroon near borders with East and Centre Provinces in a lowland, probably forested area.

The leaves of *Pavetta laxa* are similar to those of *P. longibrachiata* and *P. brachysiphon* (see discussion following the description of *P. brachysiphon*). In *P. laxa* the leaves are larger and less narrow than those of *P. brachysiphon*, however, and corollas are shorter and styles are shorter and exserted less than those of *P. longibrachiata*. *Pavetta laxa* has very small flowers except for calyx lobes larger than average in subgenus *Baconia*.

Pavetta laxa is so named for its very lax inflorescences.

16. Pavetta longibrachiata Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 75. 1934. TYPE: Cameroon. West Province (probably): Ndonge, *Ledermann 6179* (holotype, B destroyed). LECTOTYPE: Cameroon. East Province: near Bangué, mouth of Bangué River, 3°N, 15°4'E, Feb. 1911 (fl bud), *Mildbraed 4505* (lectotype, selected here, HBG).

Shrubs to 5 m. Twiglets shortly puberulent to glabrous, floriferous twiglets 4–26 cm. Leaves chartaceous to subcoriaceous, sometimes anisophyllous, top pair sometimes extremely so or reduced to one leaf; blades elliptical to obovate, oblong (or less often ovate or rotund), sometimes asymmetrical, 3.5–22 × 1.5–7.5 cm, (occasionally puberulent or partly pubescent to) normally glabrous or upper surface appearing papillate, major veins puberulent below, puberulent to glabrous above; apex acute (to less often obtuse or rounded), sometimes asymmetrical, subacuminate or with acumen 3–15 × 2–10 mm; base cuneate (to less often attenuate, rounded or cordate), sometimes asymmetrical; midrib and sometimes secondary veins prominulous below, secondary veins 4–11(–14) each side, sometimes joined 1–6 mm from margin; domatial tufts, pockets or pits in branch vein angles of midrib and often along secondary veins; nodules absent or few, scattered on blade and sometimes on midrib; fourth and higher order venation usually more obvious below than above, occasionally obvious both above and

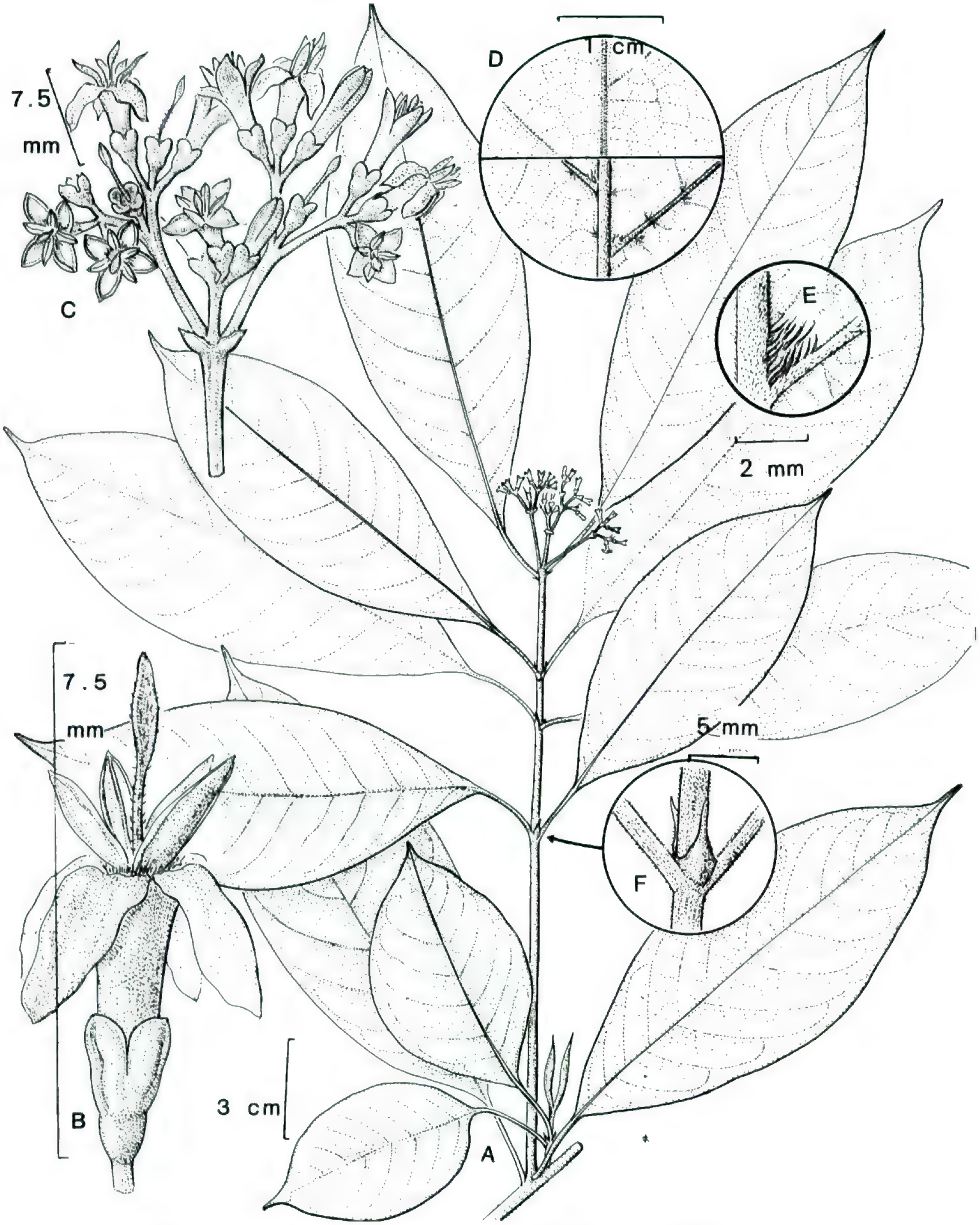


Figure 15. *Pavetta laxa* (*Letouzey 4581*, YA).—A. Habit.—B. Flower.—C. Inflorescence.—D. Leaf venation and vestiture: top half, upper surface; bottom half, lower surface.—E. Angle of secondary leaf vein below with tuft domatium.—F. Stipules.

below or neither above nor below; venation density medium to fine. Stipules cup-shaped, puberulent to subglabrous externally, pubescent to glabrous internally, awn sometimes deciduous, curved, linear or cuspidate, 1–3 × ≤1 mm. Inflorescences rotund to corymb-shaped in outline or with subunits of these shapes, 0.5–9 cm across, puberulent to subglabrous, peduncle to 45 mm or usually absent,

flowers 15–200; sheathing bracts unlobed and cup-, funnel-, (or less often saucer-)shaped or with rotund to ovate, irregular, or truncate lobes, puberulent or subglabrous externally, pubescent internally, sometimes with linear awns 0.5–5 mm, sometimes with foliar appendages 2–2.5 mm or ovate appendages 1.5–4 × 0.5–1 mm; foliar bracts usually absent, 2 mm to size and shape of normal foliage leaves if present; other bracts ± broadly obovate, to 4 mm, sometimes with 1–several fimbriae or with a ca. 1 mm awn, or fimbriae or tufts of hairs borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 0.7–1 mm long, 1.2–2 mm wide halfway up; lobes valvate, triangular, ovate, oblong, pentagonal, rotund, or subquadrate, 0.5–2 × 1 mm, pubescent to subglabrous, usually carinate, sometimes concave, rim narrowly lighter. Corolla white with green apex in bud, white in open flower; most tubes broadened from base to apex, (2–)3–8 × 0.5–1.5 mm; lobes 3–9 mm. Style clavate, pubescent to subglabrous, exserted (2–)6–10 mm. Stigma ± 2-lobed. Fruits 7–8 mm across, subglabrous or glabrous, whitish green or ash gray. Mature seeds 2 or 1, attached ca. halfway up septum, broadly concave.

Additional specimens examined. CAMEROON. **East Province:** 14 km E of Dimako, Feb. (fl), *Leeuwenberg 7785* (BR, HBG, K, MO, P, WAG, YA); 10 km S of Ndemba, Mbang-Ndemba road, May (fr), *Breteler 1451* (BR, WAG). **South Province:** Bitye, River Dja, Nov. (fl bud), *Bates 1520* (BR, MO), Feb. (fl bud & fl), *Bates 1619* (BM, MO); Méyos-Méla, 32 km ENE of Djoum, Nov. (fr), *Letouzey 8324* (BR, P). **Centre Province:** 5 km W of Mbalmayo, Feb. (fl bud), *de Wilde & de Wilde-Duyfjes 1807* (BR, P, WAG); Yaoundé (fl bud), *Zenker 759* (K, S), and see Ivory Coast specimens listed below marked "origine Yaoundé"; foot of Mt. Ngoro, 38 km N of Bafia, Apr. (young fr), *Ngameni Kamga 79* (P); Guéré road E of Yoko, Feb. (fl bud), *Letouzey 3428* (YA). **Southwest Province:** NW side of Mt. Cameroon above Koto, Mar. (fl), *Thomas 4494* (MO). IVORY COAST. Centre de Recherches Agronomiques de Bingerville, near Bingerville, cultivated, origin Yaoundé, Cameroon, Feb. (fl), *Bodard 1353* (K), Feb. (young fr), *Bodard 1356* (K).

Pavetta longibrachiata is fairly widespread in the East Province and drier forested areas of Centre and South Provinces of Cameroon, and has also been found in the Southwest Province. Although endemic to Cameroon (except for cultivated plants) based on existing collections, it is predicted from its fairly wide distribution and undercollection of neighboring countries that it will be found also south and east of Cameroon.

Pavetta longibrachiata occurs in secondary and disturbed forest understory and new growth of savanna, mostly at 550–1000 m elevations. The cultivated specimens are less robust vegetatively and reproductively than most specimens from Cameroon; they represent a rare recorded attempt to cultivate a species of subgenus *Baconia*.

Pavetta longibrachiata is most similar to *P. laxa* and *P. brachysiphon*, based upon leaf morphology features discussed following the description of *P. brachysiphon*, and is compared with those species following their descriptions. It can be distinguished from *P. cellulosa*, which it also resembles, in having nonseptate anthers, and from *P. owariensis* by its papillate or rarely pubescent upper leaf surfaces, vestiture on twiglets and stipule exteriors, and usually smaller flowers.

No duplicates of the original holotype, *Ledermann 6179* (B), have been found. Two paratypes, *Waibel 169* (B) and *Mildbraed 4505* (B), have also been destroyed; *Mildbraed 4505* (HBG) is here selected as lectotype.

17. Pavetta longistyla S. D. Manning, sp. nov. TYPE: Cameroon. West Province (probably): "route des Mbos," probably near Dschang, Mar. 1967 (fl), *Meurillon 645* (holotype, P; isotype, BR). Figure 16.

Frutex. Rami glabri. Folia glabra, apice rotundato ad obtusum, nervis secundariis utroque 5–8, domatiis nullis. Inflorescentiae in ambitu rotundatae ad subcorymbosas, 9–13 cm latae. Lobi calycini pentagonales ad ovatos vel triangularos, 1.5–3 × (0.7–)1–2 mm. Corolla tubo 6–10 mm, lobis 9–14 mm. Styli exserti 20–30 mm.

Shrubs. Twiglets glabrous, floriferous twiglets 15–18 cm and probably longer. Leaves chartaceous to subcoriaceous, glabrous, not anisophyllous; blades obovate (to less often elliptical), 5.5–19 × 2–9.5 cm; apex rounded to obtuse with acumen 2–15 × 2–12 mm; base cuneate to attenuate, sometimes asymmetrical; midrib prominulous below near base, secondary veins 5–8 each side, sometimes joined 2–9 mm from margin; domatia absent; nodules absent or along origins of some branch veins along midrib (and less often secondary veins) or in branch vein angles of midrib, fourth and higher order venation usually slightly more easily visible above but obscure on both sides; venation density medium. Stipules deciduous, cup-shaped, pubescent internally near base, glabrous externally; awn cuspidate to linear, sometimes falcate, 2–5 mm. Inflorescences rotund to subcorymb-shaped in outline, 9–13 cm across, subglabrous distally, glabrous proximally, sessile, flowers 40–60; sheathing bracts sometimes deciduous, at least sometimes rotund lobed, pubescent internally, subglabrous externally, sometimes with linear awns or foliar appendages to 3 mm; foliar bracts if present 10–25 mm; other bracts ovate, 1–3 mm, sometimes with

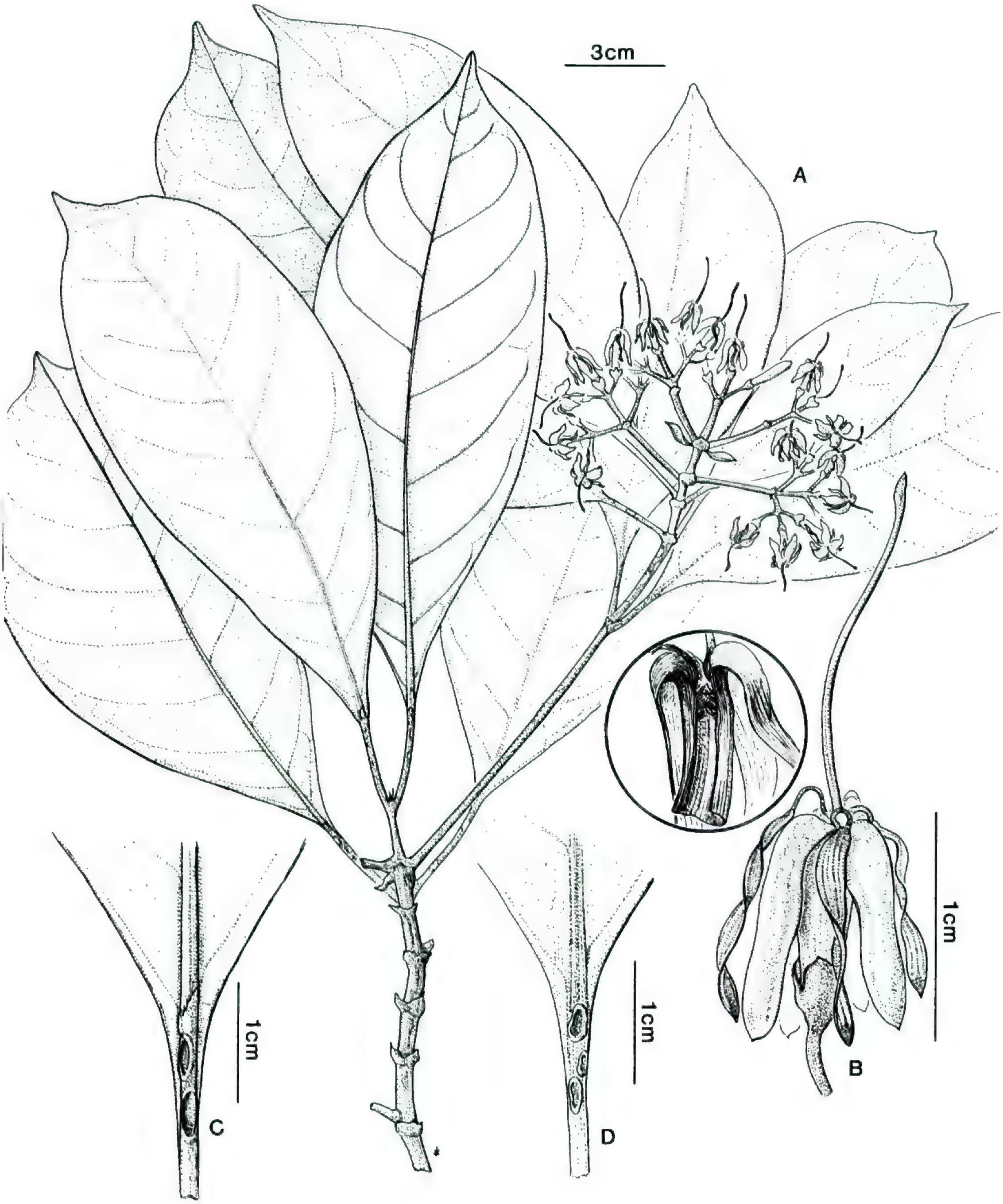


Figure 16. *Pavetta longistyla* (*Meurillon 645*, P).—A. Habit.—B. Flower and corolla opened to show beard.—C and D. Leaf bases with obscure higher order venation and lack of domatia.

several fimbriae to 2 mm, often absent at upper nodes of inflorescences; bracteoles absent. Calyx tube 1.5–2 mm long, 2–3 mm wide halfway up; lobes valvate, deltoid to pentagonal, rotund (or less commonly oblong, obovate, or ovate), 1.5–3 × (0.7–) 1–2 mm, subglabrous to glabrous, usually carinate, rim lighter. Corolla white, subcylindrical or cylindrical, tube 6–10 × 2–3 mm; lobes 9–14 mm. Style narrowly clavate, puberulent, exserted 20–30 mm. Ovules in open flower 2, white, ± ovoid, apparently attached ca. halfway up septum.

Pavetta longistyla is known only from the type collected near the western boundary of West Prov-

ince, Cameroon, in forest beside a stream at an altitude of 1100 m.

Pavetta longistyla resembles taxa of subgenus *Pavetta* in that it lacks bracteoles and its style-pollen presenters are exserted 20–30 mm, further than in any other species of subgenus *Baconia* in Cameroon. Its bearded corolla throat places it in subgenus *Baconia,* however.

Most leaves are broadly obovate and, as in *Pavetta kupensis,* leaf apices are obtuse or rounded, never acute as in most species. *Pavetta longistyla*'s large, lax inflorescences, lack of domatia, and less strongly brochidodromous venation distinguish it from *P. kupensis.* It resembles *P. mollissima* Hutch. & Dalziel, a western African species, vegetatively but is distinct from it in having less vestiture, larger flowers, and laxer inflorescences. It resembles *P. viridiloba* K. Krause and *P. molundensis* in inflorescence shape but can be distinguished from *P. viridiloba* by its smaller, usually obovate leaves and lack of vestiture and from *P. molundensis* by its larger, fewer-flowered inflorescences and obscure leaf venation.

18. Pavetta molundensis K. Krause, Bot. Jahrb. Syst. 57: 39. 1922. TYPE: Cameroon. East Province: ca. 15°22′E, 3°27′N, Bundi, formerly in Bezirk Molundu, near Yokadouma and Ngola, Mar. 1911 (fl bud), *Mildbraed 4673* (holotype, B: reported as *Mildbraed 6473,* presumably in error, destroyed; lectotype, selected here, HBG).

Pavetta insignis Bremek., Repert. Spec. Nov. Regni Veg. 37: 65. 1934. SYNTYPES: Uganda. *E. Brown 217* (K); *Mildbraed 2456* (B destroyed).

Shrubs to 6 m. Twiglets glabrous, floriferous twiglets 3–27 cm. Leaves coriaceous or subcoriaceous, sometimes anisophyllous; blades elliptical to obovate (or less often oblong or ovate), 3–30 × 1–12 cm, sometimes asymmetrical, glabrous (or blades at times subglabrous below); apex acute (or less often obtuse), sometimes asymmetrical, subacuminate or with acumen 5–15 × 4–10 mm; base cuneate to attenuate; midrib prominulous below toward base, secondary veins 6–11 each side, eucamptodromous; domatia absent or small pits, crypts, or pockets present in some branch vein angles of midrib and less often of secondary veins; nodules absent; fourth and higher order venation ± equally obvious above and below; venation density fine. Stipules usually deciduous, cup- or saucer-shaped, pubescent internally, glabrous or subglabrous externally, awn linear, ca. 1 mm. Inflorescences ± pyramidal, corymb-shaped or rotund in outline, 3–9 cm across, pubescent to puberulent distally, glabrous to puberulent proximally, sessile, flowers 100–350; sheathing bracts cup- or saucer-shaped or ovate lobed, pubescent internally, glabrous to puberulent externally, with 1–several linear awns to 3 mm or foliar appendages 2–5 mm; foliar bracts if present 1.5 cm or resembling less reduced foliage leaves; other bracts ovate, linear (or at times subquadrate or rotund), to 3 mm, sometimes with 1–several fimbriae to 1 mm or rarely an awn ca. 2 mm, or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 0.7–1.8 mm long, 2–3 mm wide halfway up; lobes valvate (or less often bases slightly overlapping), rotund (to less often oblong, ovate, obovate, long-pentagonal, deltoid, subquadrate, or occasionally 2-lobulate owing to either an emarginate apex or a cleft near base), 1–3 × 1–2 mm, pubescent, not or inconspicuously carinate, rim usually lighter. Corolla white; tube subcylindrical or cylindrical, 3–5(–8) × 1.5–2(–3) mm, lobes (5–)7–8(–11) mm. Style clavate, glabrous or subglabrous, exserted (5–)8–12 mm. Fruits 7–10 mm across, subglabrous, blue-gray or whitish. Seeds 2, attached ca. ⅔ of the way up septum, concave.

Additional specimens examined. CAMEROON. **East Province:** 5 km E of Bertoua, Dec. (fl), *Breteler 833* (BR, GH, P, WAG, YA); 50 km from Bertoua toward Abdumadjali, Dec. (fl bud and fl), *Nana 464* (BR, P, YA); 75 km N of Bertoua toward Deng Deng, Dec. (fl bud), *Nana 386* (BR, P, YA); near Deng Deng, Oct. (fr), *Nana 302* (BR, P, YA); near confluence of Lom and Djérem Rivers, ca. 250 km NE of Yaoundé, Mar. (fl bud and fl), *Mildbraed 8616* (K).

Most of the range of *Pavetta molundensis* is further east and south than Cameroon, including Sudan, Zaïre, Uganda, Tanzania (Bridson, 1978; Bridson & Verdcourt, 1988) and Central African Republic (Bridson, pers. comm.). It is thus centered in the Congolian centre of specific endemism sensu White (1979). In Cameroon it has been collected only in East Province. It grows in closed and open forest and savanna, including on pebbly soil and on laterite.

Pavetta molundensis is similar to *P. calothyrsa* and *P. robusta* except in typical calyx lobe shapes and in that it lacks bacterial nodules. Aids in recognizing *P. molundensis* are corolla lobes averaging much longer than corolla tubes and fruits with seeds attached ca. two-thirds rather than halfway up the septum. It is glabrous or nearly so vegetatively, except for stipule interiors. Vestiture is present on inflorescences, however, increasingly so toward the apex, culminating in pubescent calyx

lobes. Several collections of *P. molundensis* have dried nearly black.

Pavetta hookeriana and *P. molundensis* are compared following the description of *P. hookeriana.*

The original description of *Pavetta molundensis* lists the type as *Mildbraed 6473* rather than *4673.* However, locality and habitat data, date, and features of *4673* match those of the description. That description is referred to on the HBG isotype of *Mildbraed 4673* selected here as lectotype.

19. Pavetta mpomii S. D. Manning, sp. nov. TYPE: Cameroon. South Province: Nkolemenlong hill W of Ebianemeyong, near Nyabéssan, 60 km E of Campo, Apr. 1970 (fl bud & fl), *Letouzey 10341* (holotype, P; isotypes, BR, YA). Figure 17.

Frutices. Folia laminis super parce pubescentibus, subter glabris vel parce pubescentibus, nervis utrinque pubescentibus vel puberulis, nervis secundariis utroque 4–13. Inflorescentiae in ambitu corymbosae ad rotundatas, 3–7(–12) cm latae, pubescentes, floribus 20–125. Lobi calycini valvati vel superpositi basi, ovati (vel interdum oblongi, pentagonales, rotundati vel triangulares), 1.2–3 × 1–2 mm, pubescentes. Corolla tubo 5–8 mm, lobis 8–13 mm. Styli exserti 9–11 mm.

Shrubs to 2 m. Twiglets pubescent, floriferous twiglets 5.5–19.5 cm. Leaves chartaceous to subcoriaceous, veins pubescent or puberulent above and below, blades thinly pubescent above, glabrous or thinly pubescent below, sometimes anisophyllous; blades obovate to elliptical, oblong (or less often ovate), 3–22 × 1–9 cm; apex acute (to less often obtuse), usually with acumen 5–20 × 3–10 mm; base cuneate to obtuse (or less often attenuate or rounded), often asymmetrical; midrib prominulous or prominent below especially near base, secondary veins prominulous below, 4–13 each side, eucamptodromous (or less often brochidodromous); domatia absent or tuft or hairy pocket domatia in some branch vein angles of midrib; nodules if present few, on midrib or secondary veins (or occasionally scattered on blade); fourth and higher order venation more obvious below but often obscure below also; venation density fine. Stipules unlobed and cup-shaped (or less often compressed rotund lobed), pubescent internally and externally, awn cuspidate (or less often linear), (1–)3–7 mm. Inflorescences corymb-shaped to rotund in outline, 3–7(–12) cm across, pubescent, sessile or with peduncle to 4 mm, flowers 20–125; sheathing bracts compressed rotund lobed or unlobed and bowl-shaped, pubescent, sometimes with foliar appendages 1–4 mm long or linear awns 1–2 mm long; foliar bracts often present; other bracts linear, ovate or obovate, 0.5–1(–3) mm, sometimes with 1–several fimbriae ca. 1 mm or fimbriae or tufts of hairs borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 0.5–1.5 mm long, 1.2–2 mm wide halfway up; lobes valvate or bases overlapping, ovate (to less often oblong, pentagonal, rotund, or triangular), 1.2–3 × 1–2 mm, pubescent, sometimes carinate, rim lighter. Corolla white; tube widened from base to throat, 5–8 × 1–3 mm; lobes 8–13 mm. Style narrowly clavate, thinly pubescent to subglabrous, exserted 9–11 mm. Stigma occasionally visibly 2-lobed, lobes ca. 0.25 mm. Prefruiting ovules 2, ± reniform, attached ca. halfway up septum.

Additional specimens examined. CAMEROON. **South Province:** 10 km ESE of Campo, Mar. (fl bud), *Letouzey 9209* (P); SE slopes of Mt. Éléphant est. 10 km SE of Kribi, Feb. (fl), *Bos 6419* (WAG); Bipindi (fl), *Zenker 4569* (BM, K, MO); Lolodorf (fl), *Staudt 27* (S).

Pavetta mpomii is endemic to western South Province, Cameroon, a high rainfall area. The only elevation reported is 200 m, on a slope of Mt. Éléphant.

Pavetta mpomii is similar to *P. viridiloba* and the more southern *P. puberula* Hiern. Inconspicuous tertiary leaf venation and green calyx lobes on dry specimens characterize *P. mpomii* and *P. viridiloba* and distinguish them from *P. lasioclada* and *P. namatae* S. D. Manning.

Vestiture in *Pavetta mpomii* is less than that of *P. viridiloba,* coming closer to *P. puberula* in that respect. Leaves and inflorescences are usually smaller than in either of the other two species. Calyx lobes of *P. mpomii* are intermediate in shape. These three species are further compared following the description of *P. viridiloba.*

Pavetta mpomii is named in honor of M. M. Benoit Mpom, formerly of the National Herbarium of Cameroon, Yaoundé.

20. Pavetta muiriana S. D. Manning, sp. nov. TYPE: Cameroon. Southwest Province: Bakossi Mountains W of Bangem, Jan. 1986 (fl bud & fl), *Thomas & Mcleod 5303* (holotype, MO; isotypes, BR, FHI not seen, K, P, PRE not seen, WAG not seen). Figure 18.

Frutices. Folia costa et nervis secundariis subter prominentibus, saltem versus bases, nervis secundariis utroque (8–)11–16; domatiis nullis; nodulis nullis vel secus costam et raro nervos secundarios, inconspicuis ob pubescentiam; venis tertiariis subter prominentibus. Inflorescentiae (1–)2–4 cm latae, ± laxae, pubescentes. Lobi calycini deltoidei (ad interdum rotundato-compressi, rotundati vel breviter triangulares), 0.2–1 × 0.5–1 mm, pubescentes. Corolla tubo 3–5 mm; lobis 4–6 mm, lobis su-

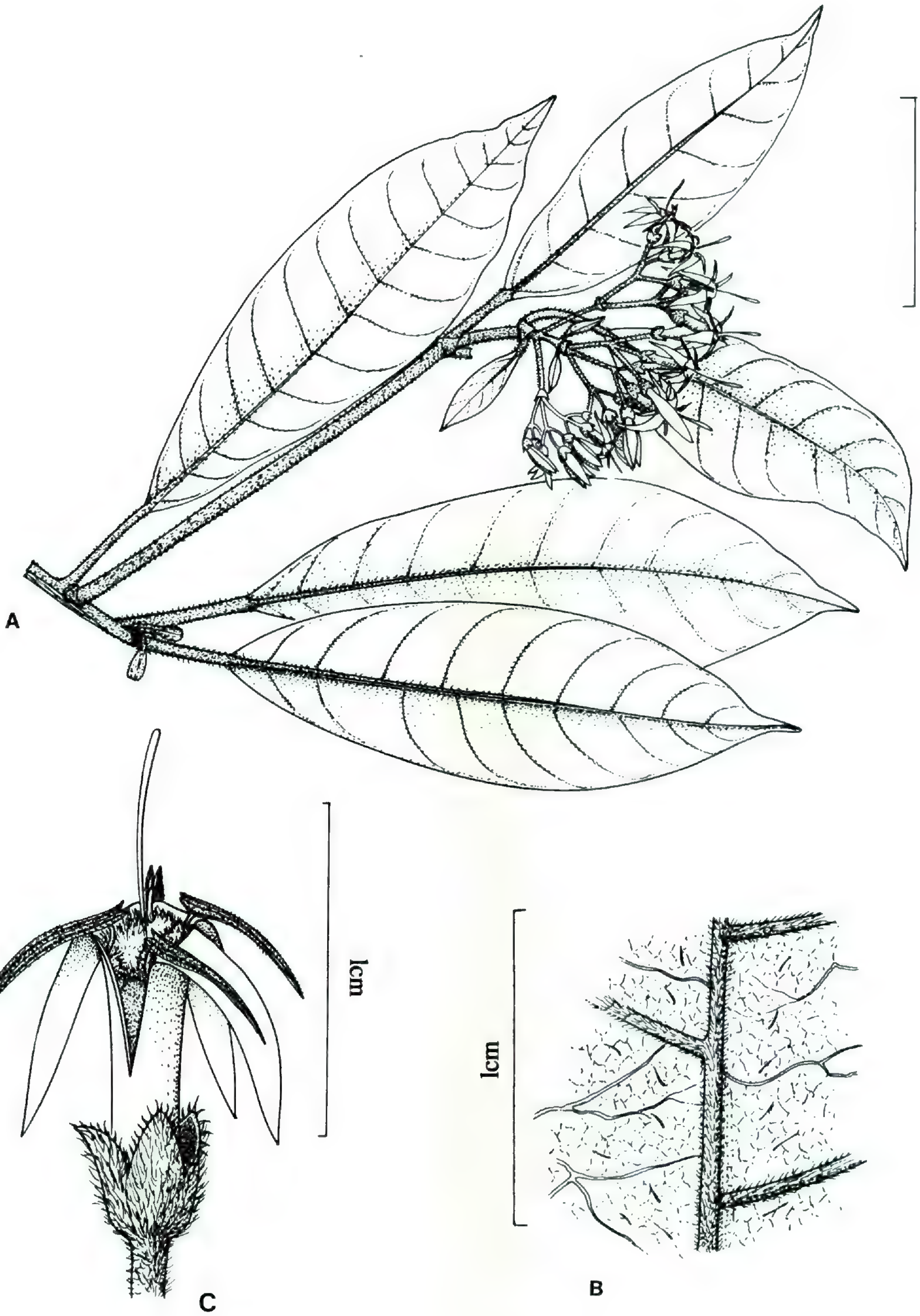


Figure 17. *Pavetta mpomii* (*Letouzey 10341*, P).—A. Habit.—B. Lower leaf surface with vestiture both on veins and lamina.—C. Flower.

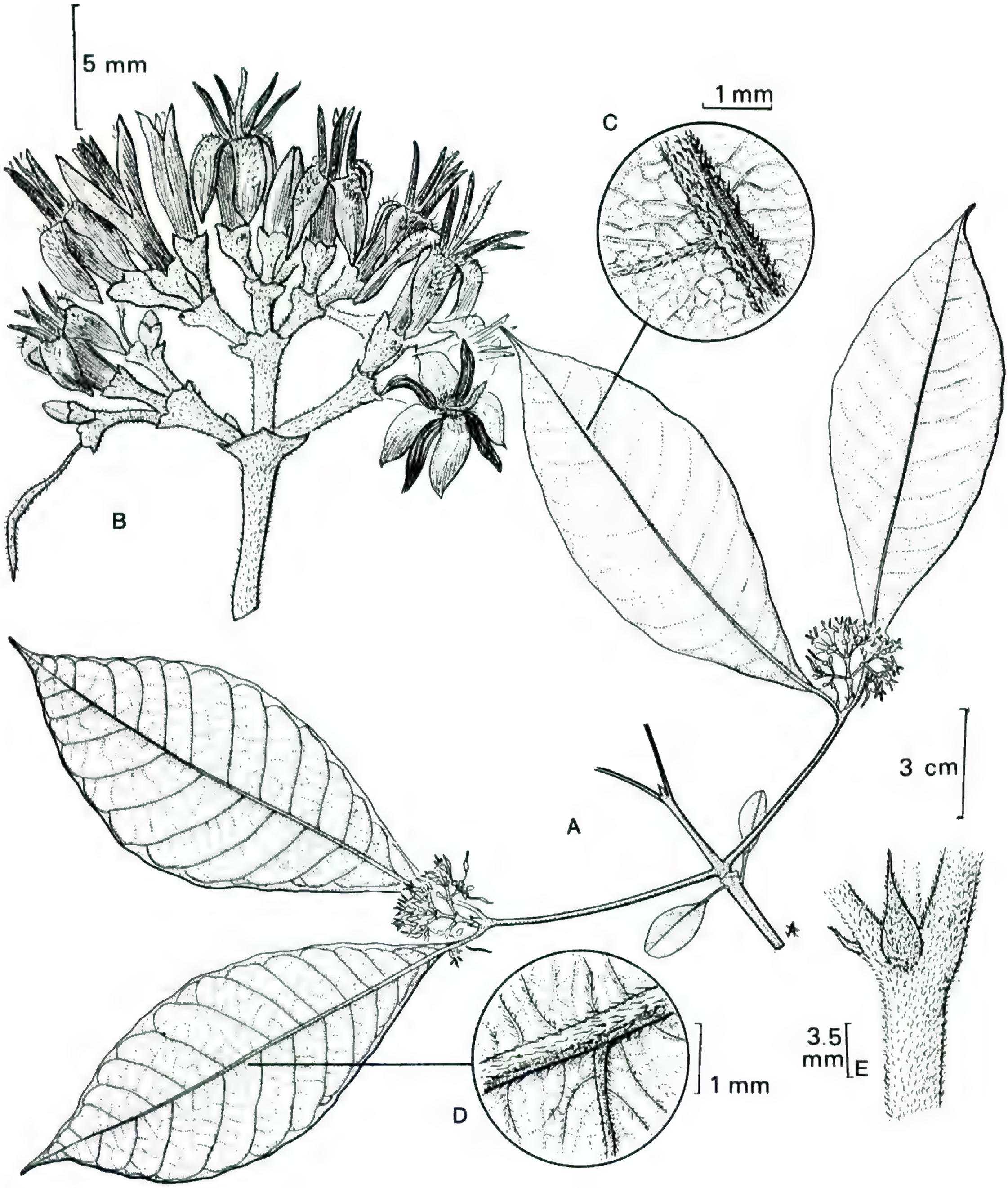


Figure 18. *Pavetta muiriana* (*Thomas 5449*, MO).—A. Habit.—B. Inflorescence.—C. Part of upper leaf surface with bacterial nodule along midrib.—D. Part of lower leaf surface.—E. Stipule.

per prope faucem pubescentibus. Anthera atra, albo-vittata. Styli exserti 3–6 mm.

Shrubs to 2 m. Twiglets pubescent, floriferous twiglets 5.5–10.5 cm. Leaves chartaceous, not anisophyllous; blades elliptic to obovate (or less often oblong), (1–)7–18 × (1–)3–8 cm, blades glabrous, major veins pubescent to subglabrous; apex acute, usually with acumen 8–13 × 2–6 mm; base cuneate to obtuse, often asymmetrical; midrib and secondary veins prominent below at least toward base, secondary veins (8–)11–16 each side, joined 1–5 mm from margin; domatia absent; nodules absent or along midrib and rarely secondary veins, inconspicuous because of vestiture; tertiary veins prominent below; fourth and higher order venation obvious, usually slightly more so above; venation density fine to very fine. Stipules deciduous, puberulent internally and externally, ± compressed

rotund lobed, awn linear, sometimes falcate, 2–5 mm or probably longer. Inflorescences pyramidal to subrotund or irregular in outline, (1–)2–4 cm across, ± lax, pubescent, sessile, not subumbellate, flowers 20–35; sheathing bracts ovate lobed or unlobed, then bowl- or saucer-shaped, pubescent externally, glabrous to pubescent internally; awns linear, 2–9 (or less often <2) mm; other bracts broadly to narrowly ovate, 0.5–2 mm, usually not fimbriate, rarely with several fimbriae to ca. 0.5 mm; bracteoles resembling smaller bracts. Calyx tube 0.5–1 mm long, 1.5–2 mm wide halfway up; lobes valvate, deltoid, subdeltoid (or less often compressed rotund, rotund, or short triangular), 0.2–1 × 0.5–1 mm, pubescent, sometimes carinate, rim not or narrowly lighter, vestiture of margins appearing lighter. Corolla white or yellow, tube cylindrical, broadened from base to throat (or less often obovate in outline), 3–5 × 1–2 mm, lobes 4–6 mm, pubescent above near throat. Anthers drying black with white stripes. Style clavate, puberulent to pubescent, exserted 3–6 mm. Prefruiting ovules 2, ± reniform, attached ca. halfway up septum.

Additional specimen examined. CAMEROON. **Southwest Province:** Lake Barombi Mbo, Kumba, Jan. (fl), *Thomas 5449* (MO).

Pavetta muiriana is known from the eastern half of Southwest Province, Cameroon. Its two collection localities are separated by ca. 100 km. One is near a volcanic crater lake at an elevation of ca. 300 m, the other is on a hillside at 1500 m. The higher elevation collection had yellow corollas, the lower had white ones.

Pavetta muiriana is compared to *P. tenuissima*, a related species, following the description of the latter.

The inflorescences and anthers (black with white stripes in open flower on herbarium sheets) of *Pavetta muiriana* resemble those of *P. neurocarpa* Bentham. Corollas of *P. muiriana* are similar to those of *P. camerounensis*, *P. rubentifolia*, *P. neurocarpa*, *P. urophylla*, and *P. tenuissima* and differ from other species in being pubescent on the upper side of lobes near throats. Nonsheathing bracts of *P. muiriana* are similar to those of *P. kribiensis*, *P. neurocarpa*, *P. tenuissima*, and *P. urophylla* and differ from other species in usually lacking fimbriae such as those in Figure 4.

Pavetta muiriana is named in honor of William Muir, former professor at Carleton College, Northfield, Minnesota, U.S.A., who developed the author's interest in botany while he was an undergraduate student, and his wife, Elizabeth, for her outstanding support of his work.

21. Pavetta namatae S. D. Manning, sp. nov. TYPE: Cameroon. Unknown location: Mar. 1918 (fl), *Gocker 18* (holotype, MO; isotype, US). Figure 19.

Frutex. Folia nervis secundariis utroque (5–)10–15; venis tertiariis interdum subter prominulis. Inflorescentiae in ambitu corymbosae ad subrotundatas vel in monades corymbosas vel subcorymbosas divisae, 6–11 cm latae, plus minusve laxae. Lobi calycini valvati, rotundati (ad interdum pentagonales, ovatos vel triangulares), 0.5–1 × 0.5–1 mm. Corolla tubo 5–7 mm, lobis 6–7 mm. Styli exserti 8–12 mm.

Shrubs ca. 6 m. Twiglets glabrous, floriferous twiglets 7–12 cm. Leaves chartaceous to coriaceous, blades and veins glabrous above, glabrous to puberulent with minute hairs below, sometimes anisophyllous; blades obovate to elliptical, 4–21 × 1.5–8 cm; apex acute to obtuse, often asymmetrical, usually with acumen 3–20 × 2–10 mm; base cuneate to attenuate, sometimes asymmetrical; midrib prominent and secondary veins prominent or prominulous below, major veins sometimes impressed above, secondary veins (5–)10–15 each side, usually joined 2–10 mm from margin; domatia present as hairy pockets in some or all branch vein angles of midrib, secondary and sometimes tertiary veins; nodules scattered on blades; tertiary veins sometimes prominulous below; fourth and higher order venation more obvious below than above; venation density fine to very fine. Stipules sometimes deciduous, shallowly cup- to saucer-shaped, pubescent internally, glabrous (to occasionally puberulent) externally, awn cuspidate, 3–5 × 1 mm, ± falcate. Inflorescences corymb-shaped to subrotund in outline or with corymb-shaped or subcorymb-shaped subunits, 6–11 cm across, sometimes ± lax, subglabrous to glabrous, peduncle absent or to 3 mm; flowers 40–200; sheathing bracts unlobed and cup- or bowl-shaped or obovate to compressed rotund lobed, pubescent internally, glabrous or subglabrous externally, usually with awns or other appendages, occasionally with fimbriae; awns ± linear, 1–2 mm; other appendages foliar, 1–5 mm or ovate, ca. 3 × 0.5–0.8 mm; fimbriae to ca. 1 mm; foliar bracts if present ca. 6 mm or resembling foliage leaves; other bracts obovate, subquadrate, linear or ovate, to 2 mm, sometimes with 1–several fimbriae to 1 mm or fimbriae borne from axis directly; bracteoles resembling smaller bracts. Calyx tube 0.7–1 mm long, 1.5–2 mm wide halfway up; lobes valvate, rotund (or less often pentagonal, ovate, or triangular), 0.5–1 × 0.5–1 mm, puberulent to subglabrous, usually carinate, rim lighter. Corolla tube constricted near base, broadened from constriction to throat, 5–7 × 0.5–1.5 mm; lobes 6–

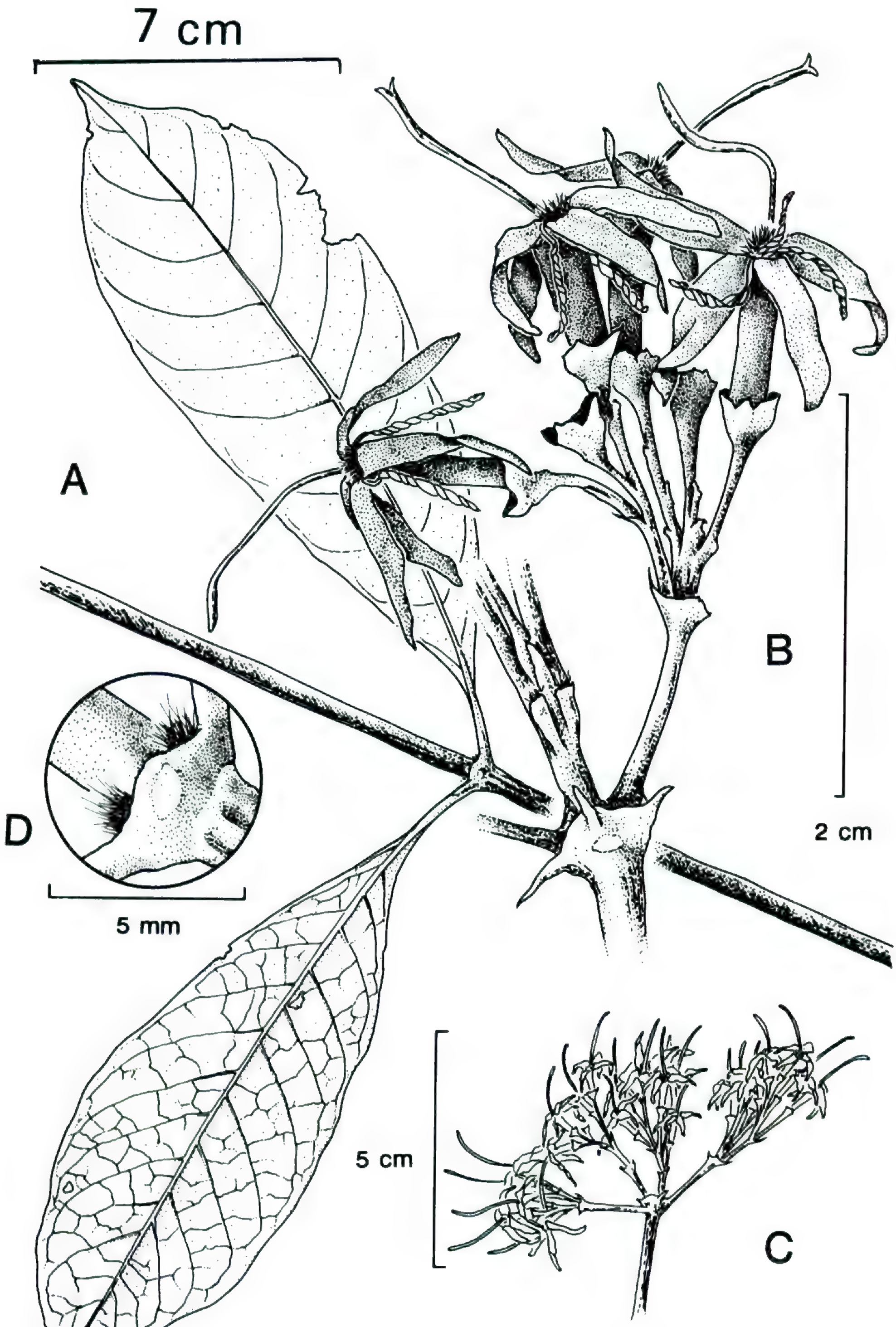


Figure 19. *Pavetta namatae* (*Gocker 18*, MO).—A. Habit.—B. Part of inflorescence.—C. Inflorescence.—D. Node with stipule base glabrous outside, hairy inside.

7 mm. Style clavate, glabrous to puberulent, exserted 8–12 mm. Stigma sometimes with 2 lobes ca. 0.5 mm. Immature fruits subglabrous. Immature seeds 2, attached ca. halfway up septum, ± reniform.

Additional specimen examined. CAMEROON. **Centre Province:** 7 km ESE of Makak, June (young fr), *Manning 2097* (MO).

Pavetta namatae is endemic to Cameroon. The only known collection locality is in south-central Centre Province.

Pavetta namatae has leaf venation very similar to that of *P. lasioclada,* including tertiary veins often prominent below. Many other features differ, however. These include leaf size, number of ovules per locule in fruits, calyx lobe features, and vestiture of stipules, sheathing bracts, leaves, inflorescences, and calyx lobes.

Pavetta namatae resembles *P. owariensis* except in leaf venation pattern. Tertiary and higher order venation of *P. owariensis* are not prominent below as in *P. namatae.* Also, there are 4–10 pairs of secondary veins in *P. owariensis,* (5–)10–15 pairs in *P. namatae.*

Pavetta namatae is named in honor of Ferdinand Namata of Makeke Camp near Mundemba, Southwest Province, Cameroon. His knowledge of the flora and fauna of Cameroon, his efforts to conserve them, and his field guidance to researchers are here recognized.

22. Pavetta neurocarpa Bentham, Niger Fl. 414. 1849. *Ixora neurocarpa* (Benth.) Kuntze, Revis. Gen. Pl. 1: 287. 1891. TYPE: Equatorial Guinea. Bioko Island, formerly Fernando Po, Nov. (1841?) (fr), *Vogel 151* (holotype, K).

Pavetta mannii Hiern, Fl. Trop. Africa 3: 169. 1877. *Ixora mannii* (Hiern) Kuntze, Revis. Gen. Pl. 1: 287. 1891. TYPE: Cameroon. Probably Southwest Province: Cameroon River or Ambas Bay, Dec. 1862 (fl), *Mann s.n.* (K, P).

Pavetta mannioides Hutch. & Dalziel, Fl. W. Trop. Africa 2: 91. 1931. Syn. nov. TYPE: Nigeria. Oban District: 1911–1912 (fl), *Talbot & Talbot s.n.* (K).

Shrubs to 4 m. Twiglets glabrous, floriferous twiglets 2–29 cm. Leaves coriaceous to subcoriaceous, sometimes anisophyllous; blades elliptical to oblong or obovate, (3–)7–35 × (1–)5–13 cm, glabrous; apex rounded to obtuse, acute (or rarely emarginate), acumen if present 5–30 × 2–12 mm; base cuneate to attenuate, sometimes strongly asymmetrical; midrib and secondary veins sometimes prominent or prominulous below, secondary veins (5–)8–16 each side, usually joined 2–15 mm from margin; domatia absent or occasionally present as small, sometimes hairy pockets in some branch vein angles of midrib; nodules scattered on blade, occasionally along midrib; fourth and higher order venation obvious or obscure above, much or slightly less obvious below; venation density fine. Stipules deciduous, remains apparently rotund to diamond or trapezoidally lobed, glabrous, awn deciduous or apparently absent. Inflorescences cymb-shaped to subrotund, pyramidal or irregular in outline or with subunits of these shapes, 0.5–13 cm across, lax to congested, glabrous (or less often subglabrous), peduncle absent or to 20 mm, flowers 3–200; sheathing bracts ovate lobed to unlobed and then cup- or saucer-shaped, sometimes subtruncate near apex, glabrous, sometimes with foliar appendages ca. 1 mm, linear awns 0.5–4 mm, or ovate awns 0.5–4 × ca. 1 mm; other bracts ovate (or less often subquadrate), concave, 0.5–2 mm, usually not fimbriate, rarely with several fimbriae or an awn to ca. 0.5 mm; bracteoles resembling smaller bracts sometimes present. Calyx tube 0.7–2 mm long, 1.2–2 mm wide halfway up; lobes valvate or almost overlapping at base, compressed rotund (to less often rotund, pentagonal, subquadrate, short triangular, or truncate), 0.2–1(–1.8) × 1 mm, glabrous (or less often subglabrous), sometimes carinate, rim lighter. Corolla white or green-white, tube cylindrical or broadened from base to throat, (0.5–)2–4(–7) × (0.5–)1–2(–3) mm; lobes 3–8 mm, pubescent above near throat or lobe vestiture sometimes nearly absent but vestiture present on filaments near their points of insertion; anthers usually drying black with white stripes; style fusiform, usually narrowly so, pubescent or puberulent, exserted (3–)6–11(–15) mm. Fruits ca. 6–10 mm across, glabrous or subglabrous, white sometimes with green vertical stripes. Mature seeds 2, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **Southwest Province:** Cameroon River or Ambas Bay, location uncertain, Dec. (fl), *Mann s.n.* (K, P); 12 km NW of Limbe, Feb. (fl), *Satabié 651* (YA); path from 4 km W of Batoke, Limbe–Idenao road, base of Mt. Cameroon, Dec. (fl), *Thomas et al. 5120* (MO), Dec. (fr), *Thomas et al. 5121* (MO); S slope of Mt. Cameroon above Batoke, Dec. (fl bud), *Thomas 2770* in part (MO), the remainder being *Pavetta rigida* Hiern and designated *2770A*; NE of Bafia, Victoria = Limbe District (fl), *Keay FHI 37533* (K); Korup National Park, Jan. (fl), *Thomas 4322* (K, MO, P, YA), Apr. (young fr), *Manning 1711* (MO), *1769* (MO); 7 km S of Mundemba, Nov. (fl bud & fr), *Manning 1035* (MO); S shore of Lake Barombi Mbo, 5 km NW of Kumba, Apr. (fr), *Manning 1779* (MO), June (fr), *Manning 2060* (MO). **South Province:** hill of Nkoltsia near Gouap, 18 km NW of Bipindi, Feb. (fl), *Villiers 794* (P). NIGERIA. **Oban District:** (fl), *Mr. and Mrs. P. A. Talbot s.n.* (K).

Most collections from Cameroon are from mature,

fully shaded, very wet forests in Southwest Province. *Pavetta neurocarpa* has also been found in wet forest in western South Province. Outside Cameroon, it has been reported only from nearby Bioko and southeastern Nigeria, where the plants formerly referred to *P. mannioides* are centered. It is a Lower Guinean species sensu White (1979). It has been collected near a lake and reported to be fragrant. Substrates reported include volcanic lava soil and rock at a hill's summit. Elevations reported are from 50 to 800 m, mostly toward the lower end of the range.

Pavetta neurocarpa is characterized by glabrous inflorescences usually drying black with strongly concave, sometimes almost boat-shaped bracts, which are glabrous internally. Occasionally, corolla tubes are shorter than 1 mm, though normally they are 2–4 mm long. Relatively unusual features *P. neurocarpa* shares with a few other species follow the description of *P. muiriana*.

Bremekamp (1934) and others maintained a separate species, *Pavetta mannioides*, for specimens with smaller, contracted inflorescences with smaller and fewer flowers than *P. neurocarpa*. Recent collections (*Satabié 651* and *Thomas 4322*) show variation sufficient to combine these species into one taxon.

23. Pavetta owariensis Palisot de Beauvois, Fl. d'Oware et de Benin, en Afrique 1: 87, t. 52. 1806. TYPE: Nigeria. Between Oware and Buonopozo (fl), *Palisot de Beauvois s.n.* (holotype, P).

KEY TO THE VARIETIES OF *PAVETTA OWARIENSIS* IN CAMEROON

1. Fourth and higher order leaf venation obscure or invisible below 2
1. At least some leaves with fourth and higher order leaf venation not obscure or invisible below 3
2(1). Calyces persistent in mature fruit; plants so far known only from Southwest Province ..... var. *satabiei*
2. Calyces not persistent in mature fruit; plants so far known only from South, Littoral, and Centre Provinces ..... var. *opaca*
3(1). Domatia absent from secondary veins and absent along most midribs ..... var. *glaucescens*
3. Domatia present along midrib and some secondary veins ..... var. *owariensis*

a. **Pavetta owariensis** var. **owariensis**

Pavetta smythei Hutch. & Dalziel, Fl. W. Trop. Africa 2: 92. 1931. TYPE: Sierra Leone. Fundu, Jan. 1908 (fl & fr), *Smythe 214* (K).

Pavetta eketensis Bremek., Repert. Spec. Nov. Regni Veg. 37: 75. 1934. TYPE: Nigeria. Eket District, 1912–1913 (fl), *Talbot & Talbot s.n.* (holotype, BM; isotype, K).

Pavetta nigritana Bremek., Repert. Spec. Nov. Regni Veg. 47: 20. 1939. TYPE: Nigeria. Sapoba (fl), *Kennedy 2346* (K).

Shrubs or small trees to 8 m. Twiglets glabrous to puberulent, floriferous twiglets 11.5–19 cm. Leaves chartaceous, sometimes anisophyllous; blades elliptical to ovate, obovate or oblong, (2–)9–16(–25) × (1–)3.5–6.5(–9) cm, glabrous except major veins and margins sometimes subglabrous, apex acute or obtuse, often asymmetrical, with acumen 3–12 × 2.5–7 mm; base attenuate to cuneate, sometimes asymmetrical; midrib prominulous below toward base, secondary veins 4–9 each side, eucamptodromous; usually hairy, crescent-shaped pocket domatia or pit or tuft domatia in most branch vein angles of midrib, sometimes along secondary veins; nodules scattered on blades or near midrib; fourth and higher order venation obvious above and below; venation density coarse. Stipules sometimes deciduous, rotund to triangular lobed, pubescent internally at least near base, subglabrous externally; awn cuspidate to linear, 1–3 mm. Inflorescences 3–6 cm across, subrotund to subpyramidal or cruciform in outline, sometimes lax, puberulent, peduncle sometimes with sheathing bracts along its length as well as at base, to 10 mm; subunits sometimes inverted pyramidal in outline; flowers 20–125; sheathing bracts triangular to rotund lobed or unlobed and saucer-shaped, puberulent to subglabrous externally, pubescent internally; awns ovate or linear, 1 mm; other bracts ovate or linear, to 2 mm, sometimes with 1–several fimbriae to 1 mm, or tufts of hair or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 0.7–1.5 mm long, 1.5–2 mm wide halfway up; lobes valvate (or bases less often slightly overlapping), rotund, triangular, pentagonal (or less often oblong or ovate), 0.5–2 × 0.5–1.8 mm, puberulent, sometimes carinate, rim usually lighter. Corolla white; tube broadened from base to apex, 3.5–6 × 0.7–2.5 mm; lobes 4–7 mm. Style narrowly clavate, pubescent or puberulent, exserted 7–9 mm. Pre-fruiting ovules 2, attached ca. halfway up septum, reniform.

Additional specimens examined. CAMEROON. **Southwest Province:** southern end of Korup National Park, Mar. (fl), *Thomas & McLeod 5823* (K, MO).

b. **Pavetta owariensis** var. **opaca** S. D. Manning, var. nov. TYPE: Cameroon. South Province: 60 km S of Edéa, S of Mboké, Mar. 1965 (fl), *Leeuwenberg 5555* (holotype, P; isotypes, BR, K, MO, WAG). Figure 20.

A varietate *owariensi* domatiis interdum nullis, inter-

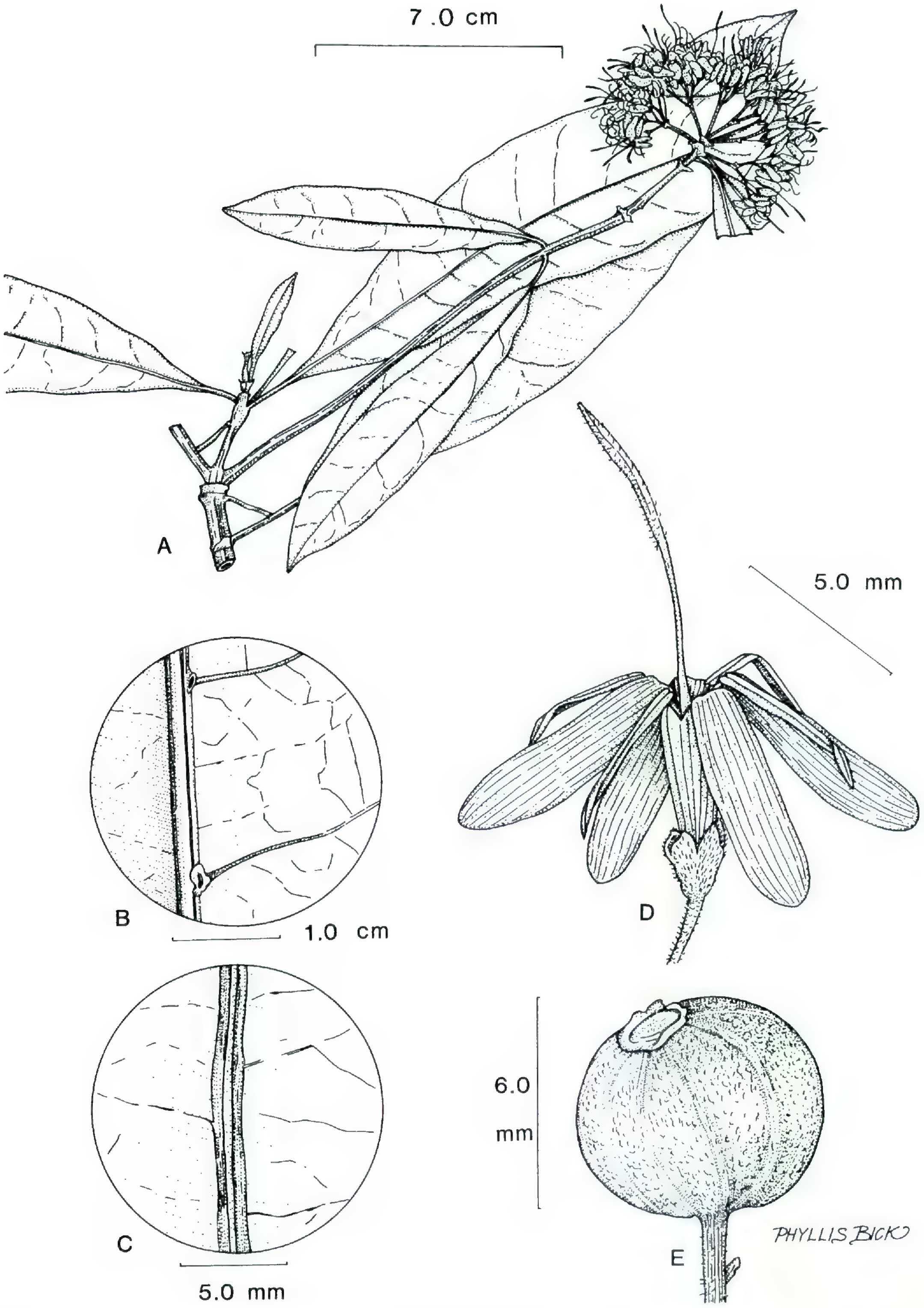


Figure 20. *Pavetta owariensis* var. *opaca* (A–D, *Leeuwenberg 5555*, P; E, *de Wilde & de Wilde-Duyfjes 1538*, MO).—A. Habit.—B. Part of lower leaf surface with domatia and showing obscure venation.—C. Part of upper leaf surface with bacterial nodules (elongated darker areas) along midrib.—D. Flower.—E. Fruit lacking persistent calyx.

dum secus costam et rare secus nervos secundarios; reticulo tenui, venulis utrinque obscuris vel invisibilibus differt. Inflorescentiae 2–15 cm latae; corolla tubo (3–)5–9 mm longo, lobis 6–11 mm longis; styli exserti (6–)10–15 mm.

Shrubs or small trees to 15 m tall. Floriferous twiglets glabrous, to 37 cm. Leaves sometimes coriaceous, no ovate blades seen; apex occasionally rounded; acumen to 23 × 12 mm; base sometimes obtuse, only slightly if at all asymmetrical; midrib prominent below at least toward base, domatia absent or present as crypts in some branch vein angles of midrib and occasionally on secondary veins, often puberulent; nodules along midrib and on blade, sometimes rare; venation density fine; fourth and higher order venation obscure or invisible above and below; stipules cup-shaped, glabrous externally, awn to 4 mm. Inflorescences corymb-shaped to pyramidal or rotund in outline, 2–15 cm across, sometimes subglabrous proximally, sessile or subsessile, flowers to 350 per inflorescence; sheathing bracts sometimes with linear awns to 2 mm or foliar appendages to 3 mm; foliar bracts sometimes present; other bracts concave, irregular or obovate; calyx tube to 1.8 mm long and to 2.5 mm wide halfway up; lobes 1–3 × 1–2 mm, subglabrous to pubescent; corolla tube subcylindrical or cylindrical, (3–)5–9 × 1–3 mm, lobes 6–11 mm; style subglabrous to pubescent, exserted ca. (6–)10–15 mm. Fruits ca. 8 mm across, subglobose, puberulent to glabrous, whitish, gray-green, or light green with darker green streaks, without persistent calyx. Seeds 2 or 1, slightly concave when immature. Other character states within ranges described above for variety *owariensis*.

The most obvious distinguishing feature of variety *opaca* is the obscure leaf venation above and below as a result of its thick, sometimes brittle leaves. Although this also occurs in variety *satabiei*, the calyx does not persist in fruit in variety *opaca* as it does in variety *satabiei*. The tallest representative of subgenus *Baconia* in Cameroon belongs to variety *opaca*.

Additional specimens examined. CAMEROON. **South Province:** Bipindi (fr & vegetative), *Zenker 2554* (BR, HBG, MO, S, W, WAG); Bitye (fl), *Bates 1210* (BM, labeled "Bitye, Yaunde"; MO, labeled "Bitye River"). **Littoral Province:** Tissongo, July (fr), *DBM/JSG = McKey & Gartlan 109* (K). **Littoral Province (Centre?):** Kéllé River ca. 50 km NW of Eséka, Nov. (fl bud & fr), *de Wilde & de Wilde-Duyfjes 1295* (K, MO, WAG). **Centre Province:** Yaoundé (fl), *Zenker & Staudt 278* (K), *543* (BM); 16 km from Eséka, chantier de la SBC de Badjob, Feb. (fr), *Mpom 202* (BR, YA); 40 km S of Badjob, 50 km SW of Eséka near Nyong River, Dec. (fr), *de Wilde & de Wilde-Duyfjes 1538* (B, BR, K, MO, WAG, YA); Son Mbong, 50 km SW of Eséka, Dec. (fl bud & fr), *Bamps 1378* (BR, P, YA); 5 km W of Son Mbong, Mar. (fl), *Leeuwenberg 5069* (BR, HBG, MO, WAG, YA).

c. Pavetta owariensis var. **glaucescens** (Hiern) S. D. Manning, comb. nov. Basionym: *Pavetta glaucescens* Hiern, Fl. Trop. Africa 3: 171. 1877. *Ixora glaucescens* (Hiern) Kuntze, Revis. Gen. Pl. 1: 286. 1891. TYPE: Equatorial Guinea. Bioko Island, formerly Fernando Po, rec'd. June 1862 (fl), *Mann s.n.* (holotype, K).

Pavetta chionantha K. Schum. & K. Krause, Bot. Jahrb. Syst. 39: 552–553. 1907. TYPE: Cameroon. South Province: Bipindi, Mar. 1900 (fl bud & fl), *Zenker 2254* (syntypes, B destroyed, BM, HBG, S, W).

Shrubs to 4 m. Floriferous twiglets 6–27 cm. Leaves membranaceous to coriaceous, blades to 25 × 10 cm, apex occasionally rounded or emarginate, acumen to 21 × 12 mm or occasionally absent, domatia absent from secondary veins and usually from midrib, venation sometimes brochidodromous, venation density medium, fourth and higher order venation often obscure above; stipules cup-shaped, glabrous externally, awn to 4 mm. Inflorescences sometimes trapezoidal or corymb-shaped in outline, to 16 cm across, sometimes subglabrous, peduncle absent or ca. 3 mm; sheathing bracts sometimes cup-shaped, their internal vestiture often extending beyond margin, with linear awns to 2 mm and sometimes foliar appendages 3–5 mm; foliar bracts resembling normal or slightly reduced foliage leaves sometimes present; calyx lobes mostly ovate, ca. 1–4 mm long, sometimes subglabrous, margin ciliate; corolla tube 5–8 mm, sometimes cylindrical, lobes 6–12 mm, tips green in bud; style exserted 9–18 mm, sometimes glabrous. Fruits and seeds similar to those of variety *opaca*. Other character states within ranges described above for variety *owariensis*.

Of the above described features, the ones most reliably distinguishing variety *glaucescens* from variety *owariensis* in Cameroon are: fourth and higher order venation often obscure above, domatia absent from secondary veins and usually from the midrib, calyx lobes mostly ovate, corollas larger, and styles further exserted.

Additional specimens examined. CAMEROON. **Southwest Province:** ca. 25 km N of Kumba on Kumba-Mamfe road, July (fr), *Nemba & Thomas 140* (MO); Southern Bakundu Forest Reserve, Mar. (fl), *Onochie et al. FHI 31199* (K); Southern Bakundu Forest Reserve, Bopo-Banga path, Feb. (fl), *Binuyo & Daramola FHI 35576* (K); Southern Bakundu Forest Reserve, path from beacon 45–44, Apr. (fl), *Ejiofor FHI 29306* (K); Southern Bakundu Forest Reserve, near Kindonge Camp ca. 20 km SSW of Kumba, Apr. (fl), *Manning 1684* (MO), Apr. (young fr), *Manning 1680* (MO); Barombi Kang near Kum-

ba, Feb. (fl), *Thomas 4367* (MO), June (fr), *Thomas 7076* (MO); Lake Barombi Mbo ca. 5 km NW of Kumba, Apr. (fl & young fr), *Manning 1785* (MO), Nov. (fr), *Manning 703, 792, 819, 820* (all MO), June (fr), *Manning 2059* (MO), Mar. (fr), *Nemba & Thomas 76* (MO); southern end of Korup National Park, Mar. (fl bud), *Thomas & McLeod 5826* (BR, MO), Apr. (fl), *Thomas 4724* (MO); southwestern corner of Korup National Park, June (fr), *Thomas 8108* (MO); Mundemba, Mar. (fl), *Thomas 6798* (MO); Rio del Rey, June (fl), *Johnston s.n.* (K). **Littoral Province:** S of Nkongsamba, Dec. (fl bud), *de Wit 306* (WAG). **Centre Province:** Yaoundé (vegetative), *Zenker 700* (K lower part of sheet only; not upper part of K sheet or NY, P, or S, which are *Pavetta calothyrsa*). **South Province:** Bipindi, Mar. (fl bud & fl), *Zenker 2254* (BM, HBG, S, W).

d. Pavetta owariensis var. **satabiei** S. D. Manning, var. nov. TYPE: Cameroon. Southwest Province: Butu–Dikome Balue Road ca. 34 km NW of Kumba, Mar. 1976 (fl bud & fl), *Satabié 252* (holotype, BR; isotype, YA). Figure 21.

A varietate *opaca* fructu maturo cum calyce persistenti differt.

Similar to variety *opaca* except calyces persistent in fruit. Also, in variety *satabiei* the tallest reported representative is 5 m, no domatia have been seen, and fruits to ca. 10 mm across have been seen.

Additional specimens examined. CAMEROON. **Southwest Province:** around Ehumseh, Ntehol and Mejelet, W of Bangem, June (fr), *Etuge & Thomas 178* (BR, MO); path from Ndibisi to Mejelet, W of Bangem, June (fr), *Etuge & Thomas 534* (MO).

In Cameroon, *Pavetta owariensis* var. *owariensis* is known only from Korup National Park in southwestern Southwest Province. It is centered west of Cameroon in the Upper and Lower Guinean subcentres of specific endemism sensu White (1979). It also has been reported from Bioko and Gabon. Variety *opaca* is endemic to Cameroon and is fairly widespread in Littoral, Centre, and South Provinces. Variety *glaucescens* occurs in Cameroon, southeastern Nigeria, Bioko, and reportedly in Gabon, Cabinda (Angola), Rio Muni (Equatorial Guinea), and Congo (Hepper & Keay, 1963). Its distribution thus is centered in the Lower Guinea centre of specific endemism sensu White (1979), overlapping that of the more west-centered variety *owariensis* in southern Nigeria, Cameroon, and Bioko. In Cameroon, though most collections of variety *glaucescens* are from southern Southwest Province, others are from widely scattered locations in Centre, South, and Littoral Provinces. Variety *satabiei* is endemic to Cameroon's Southwest Province.

Pavetta owariensis occurs in mature and secondary forest and at forest edges. Varieties *glaucescens*, *opaca*, and *owariensis* are lowland taxa; variety *opaca* has also been found at 800 m. Variety *satabiei* has been found so far only at elevations between 800 and 1400 m. Reported heights of varieties *opaca* and *owariensis* include plants taller than in the other two varieties or in most other species of subgenus *Baconia* in Cameroon.

Intermediates nearly bridge the gaps between the varieties recognized here, which are thus a compromise between distinctions that are too fine at the species level and a failure to recognize taxonomically the differences that do exist.

Although *Pavetta owariensis* is variable as interpreted here, the spreading, sometimes lax inflorescences, sometimes profuse in varieties *glaucescens*, *opaca*, and *satabiei*, and medium to large flowers of *Pavetta owariensis* span the varieties recognized and distinguish *P. owariensis* from otherwise similar species such as *P. grossissima* and *P. gabonica*, which have smaller inflorescences. Calyx lobes are never subquadrate (Fig. 5) as in *P. calothyrsa*. They are never compressed (Fig. 5) and are 1 mm or more long. Their bases overlap less than 10% of the time, distinguishing *P. owariensis* from *P. corymbosa*. Lack of papillae or vestiture on upper leaf surfaces distinguishes it from most specimens of *P. longibrachiata*, and leaf venation and domatia patterns in the latter species are distinct from those found in any of the varieties of *P. owariensis*. *Pavetta namatae* differs in having tertiary leaf veins often prominent below and in having more secondary veins.

The former *Pavetta glaucescens*, including the former *P. hygrophytica* and newer collections, remains intact at the varietal level. Variety *opaca* is so named for its obscure or invisible higher order venation both above and below. Variety *satabiei* is named in honor of Benoit Satabié, director of the National Herbarium of Cameroon, who collected the first known and type specimen of the variety.

24. Pavetta robusta Bremekamp, Repert. Spec. Nov. Regni Veg. 47: 19. 1939. TYPE: Gabon. Haute-Ngounyé, Poungui, Mar. 1927 (fl bud & fl), *Le Testu 6420* (holotype, BM; isotypes, BR, MO, P).

Shrubs ca. 5 m. Twiglets glabrous, floriferous twiglets 2.5–18 cm. Leaves coriaceous to subcoriaceous, glabrous, occasionally anisophyllous; blades oblong to obovate or elliptical, 5–28 × 2–13 cm; apex obtuse to acute, rounded (or rarely emarginate), acumen if present 4–15 × 3–10 mm, base cuneate or attenuate, sometimes asymmetrical, midrib prominulous below toward base, midrib and secondary veins often impressed above, secondary

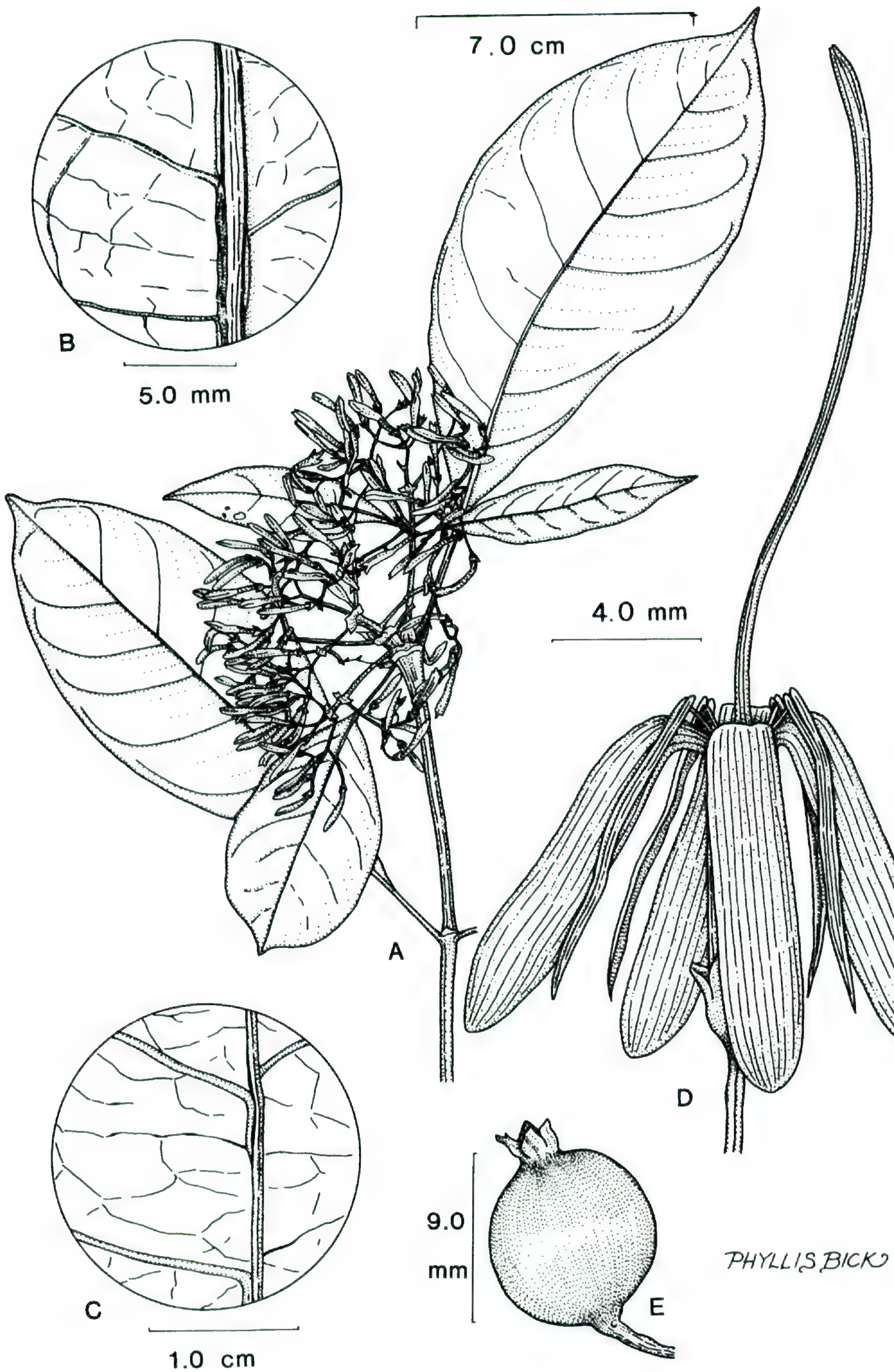


Figure 21. *Pavetta owariensis* var. *satabiei* (A–D, *Satabié 252*, BR; E, *Etuge & Thomas 178*, MO).—A. Habit.—B. Part of upper leaf surface with bacterial nodules along midrib.—C. Part of lower leaf surface without domatia.—D. Flower.—E. Fruit with persistent calyx.

veins 5–9 each side, eucamptodromous or brochidodromous, often sparingly pubescent, often crescent-shaped pocket or sometimes pit domatia in some branch vein angles of midrib; nodules scattered on blade, rarely on midrib; fourth and higher order venation usually slightly more obvious above; venation density fine. Stipules rotund lobed, glabrous externally and internally at least above the base, awn deciduous. Inflorescences corymb-shaped to subrotund or pyramidal in outline, 4–14 cm across, subglabrous to puberulent distally, subglabrous to glabrous proximally, sessile except leafless lateral inflorescences from node below main inflorescence, if considered separate, with peduncles to 4 cm; flowers 75–400, fragrant; sheathing bracts rotund or ovate lobed, glabrous to pubescent near base internally, glabrous externally, awns deciduous, ± ovate to linear, ≥1 mm; foliar bracts if present resembling small foliage leaves except base sometimes auriculate; other bracts ovate to rotund lobed, to 3.5 mm, sometimes with 1–several fimbriae to 2 mm or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 1–1.8 mm long, 1.2–2 mm wide halfway up; lobes valvate or bases overlapping, subquadrate (to sometimes obovate, compressed rotund, rotund, truncate or shallowly 2-lobulate), 0.2–1 × 1–2 mm, glabrous, not or inconspicuously carinate, rim sometimes lighter. Corolla white, tube broadening from base or slightly above base to apex, 5–9 × 1–2.5 mm; lobes 5–9 mm. Style clavate, subglabrous to pubescent, exserted (4–)7–10 mm. Stigma 2-lobed, lobes rarely spreading up to 2 mm. Ovules in open flower 2, ± reniform, one on each side of septum.

Additional specimens examined. CAMEROON. **South Province:** Bitye (fl bud & fl), *Bates 1046* (BM, MO; both labeled "Bitye, Yaunde").

The only collection of *Pavetta robusta* from Cameroon is apparently from lowland forest. The species also occurs in Gabon. Its large leaves and large, profuse, many-flowered inflorescences fit its name excellently. Comparisons of *P. robusta* to the similar *P. calothyrsa* and *P. molundensis* follow the descriptions of those species. It is similar to *P. corymbosa* in having calyx lobe bases overlapping more than 10% of the time. However, calyx lobes are rarely longer than 1 mm in *P. robusta*, rarely as short as 1 mm in *P. corymbosa*. Calyx lobes are usually subquadrate (Fig. 5) in *P. robusta*, usually rotund and rarely subquadrate in *P. corymbosa*. Leaves and inflorescences also are larger on average in *P. robusta* than in *P. corymbosa*.

25. Pavetta rubentifolia S. D. Manning, sp. nov. TYPE: Cameroon. Southwest Province: Bakossi Mountains W of Bangem, Jan. 1986 (fl), *Thomas & McLeod 5343* (holotype, MO; isotype, YA not seen). Figure 22.

Frutex. Folia marronina, coriacea, glabra; nervis secundariis utroque 8–13; domatiis nullis; nodulis nullis. Inflorescentiae in ambitu subrotundatae ad subcorymbosas, 0.5–1.5 cm latae. Lobi calycini breviter triangulares, rotundato-compressi (vel interdum deltoidei), ca. 0.2–0.5 × 1 mm, glabri. Corolla tubo 3–4 mm; lobis 3–5 mm, super prope faucem pubescentibus. Styli exserti 3–5 mm.

Shrub 1 m. Twiglets glabrous, floriferous twiglets ca. 14 cm. Leaves maroon, coriaceous, glabrous, not or hardly anisophyllous; blades oblong to elliptic or obovate, 13–16 × 3.5–4.5 cm; apex acute, subacuminate or with acumen 8–15 × 3–5 mm; base cuneate to attenuate, sometimes asymmetrical; midrib sometimes prominulous below toward base, secondary veins 8–13 each side, usually eucamptodromous; domatia absent; nodules absent; fourth and higher order venation usually somewhat more obvious above; venation density coarse. Stipules deciduous, cup-shaped, glabrous. Inflorescences subrotund to subcorymb-shaped in outline, 0.5–1.5 cm across, subglabrous to puberulent except peduncle glabrous, peduncle 4 mm, flowers 20–35; sheathing bracts unlobed and cup- or saucer-shaped or broadly lobed, glabrous, awns linear, ca. 1 mm; other bracts ± ovate to obovate or linear, to 2 mm, sometimes with 1–several fimbriae ca. 1 mm; bracteoles if present resembling smaller bracts or fimbriae borne from pedicels directly. Calyx tube 0.7–1 mm long, 1.7–2 mm wide halfway up; lobes valvate, short triangular, compressed rotund (or less often deltoid), ca. 0.2–0.5 × 1 mm, glabrous, not (or inconspicuously) carinate, rim narrowly lighter. Corolla white; tube cylindrical or subcylindrical, 3–4 × 1–1.5 mm; lobes 3–5 mm, pubescent above near throat. Style narrowly clavate, puberulent, exserted 3–5 mm.

Pavetta rubentifolia is endemic to eastern Southwest Province, Cameroon. It is a montane forest shrub collected at an elevation of between 800 and 1600 m.

Pavetta rubentifolia is characterized by its maroon-coriaceous leaves, very small flowers, and very small but not subumbellate inflorescences. It is distinct from other Cameroon specimens, but similar to *P. ixorifolia* Bremekamp s. str., a species occurring west of Cameroon, and to *P. nitidula* s. str., which occurs south of Cameroon. *Pavetta ixorifolia* s. str. and *P. nitidula* s. str. lack the elongate acumens sometimes found in *P. rubentifolia*. Some

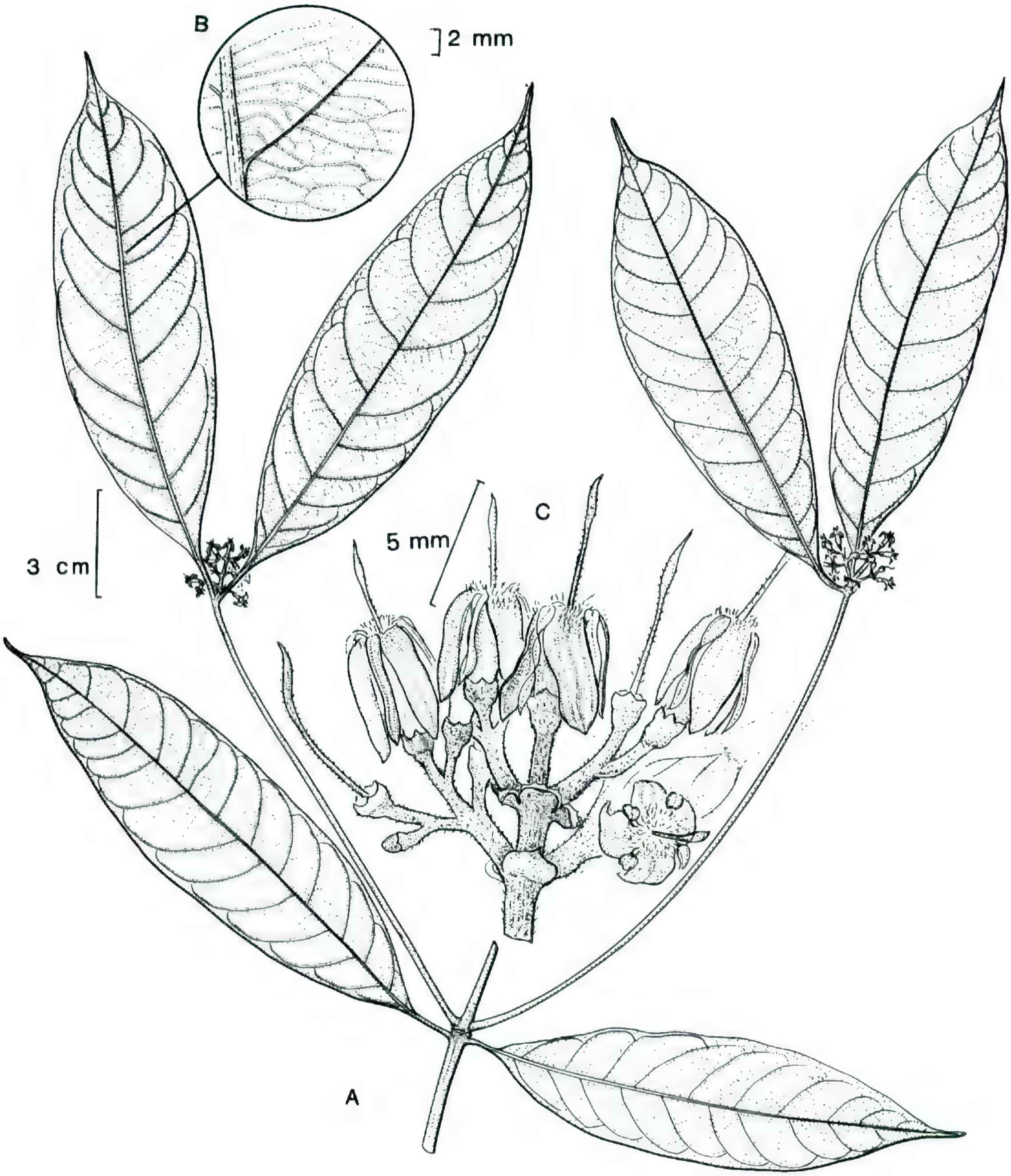


Figure 22. *Pavetta rubentifolia* (*Thomas & McLeod 5343*, MO).—A. Habit.—B. Details of leaf venation.—C. Inflorescence.

Cameroon collections have previously been identified on herbarium sheets as *P. nitidula* and others as *P. ixorifolia*, but those all belong to other species.

Pavetta rubentifolia resembles *P. camerounensis* in having corolla throat beards extending onto the upper corolla lobe surfaces. These species differ, however, in that the inflorescences of *P. rubentifolia*, while very small, are not subumbellate and in the normally shorter, narrower maroon leaves of *P. rubentifolia*.

Pavetta rubentifolia is so named because of the maroon color of its leaves as seen in the field.

26. Pavetta staudtii Hutchinson & Dalziel, Fl. W. Trop. Africa 2: 91. 1931. TYPE: Cameroon.

Southwest Province: Kumba, formerly Johann-Albrechtshöhe, 1896 (fl bud & fl), *Staudt 599* (holotype, K; isotypes, P, S).

Shrubs to 6 m. Twiglets glabrous, floriferous twiglets (4–)6–30 cm. Leaves subcoriaceous to coriaceous, glabrous, sometimes anisophyllous; blades elliptic to obovate (or less often ovate or oblong), 2–20 × 1–7.5 cm; apex acute to obtuse or rounded, sometimes asymmetrical, usually with acumen (2–)5–25(–35) × (1–)2–12 mm; base cuneate (to less often rounded, attenuate, or cordate), often asymmetrical; midrib and secondary veins prominulous or subprominulous below, secondary veins (3–)5–10 each side, sometimes joined 2–10 mm from margin; pit, pocket, or crypt domatia in branch vein angles of midrib and rarely of some secondary veins, usually pubescent; nodules mostly pustuliform, often numerous and conspicuous, scattered on blade and not usually along midrib or secondary veins; fourth and higher order venation rather obscure above, usually slightly more obvious below; venation density medium. Stipules cup- shaped, glabrous externally and above base internally, sheath often ± triangular lobed and extending to 3 mm above node, awn deciduous, linear to cuspidate, 1–3 mm. Inflorescences corymb- or subcorymb-shaped in outline, 1–8 cm across, puberulent to subglabrous distally, subglabrous (to less often glabrous) proximally, peduncle to 20 mm usually present, sometimes with a sheathing bract ca. halfway up, flowers (10–)20–100(–200); sheathing bracts rotund to elliptic lobed to unlobed and saucer- or cup-shaped, glabrous (to sometimes pubescent at base internally), with linear awns 1–2 mm or occasionally foliar appendages 2–5 mm; other bracts ovate to obovate (or less often linear), to 2 mm, sometimes with 1–several fimbriae to ca. 1 mm long, or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 0.5–1 mm long, 1.2–1.5 mm wide halfway up; lobes valvate or overlapping in bud, not overlapping at bases in open flowers, subquadrate (to less often rotund, pentagonal, or shallowly 2–3 lobulate), 0.2–1 × 0.7–1.5 mm (or occasionally truncate at base), glabrous to subglabrous, sometimes carinate, rim lighter. Corolla white or creamy white, tube broadening from base to throat, 4–11 × 0.7–2.5 mm; lobes sometimes green tipped or margined, 5–10 mm. Style clavate, pubescent (to less often subglabrous), exserted 6–12(–15) mm. Stigma sometimes narrowly 2-lobed, lobes 1–2 mm. Fruits ca. 7–10 mm across, glabrous, white, whitish, brown, light green, or gray with dark or glaucous green vertical stripes. Ovules 2, sometimes pendent in flower bud, seeds 2 or 1, concave, attached ca. halfway up septum.

Additional specimens examined. CAMEROON. **Southwest Province:** Nganjo, W bank of Meme River on Kumba–Mbonge road, Feb. (fl bud), *Thomas & Nemba 5664* (MO); Kindonge Camp, Southern Bakundu Forest Reserve ca. 20 km SSW of Kumba, Apr. (fl), *Manning 1685* (MO); 5 km W of Kumba, Nov. (fr), *Manning 739* (MO); path from Mejelet-Ehumseh to Mualong and Ndibise, ca. 5 km W of Bangem, Jan. (fr), *Etuge & Thomas 474* (MO). **Littoral Province:** bank of Mahone River, km 4 Eboné-Ekomtolo road, ca. 10 km S of Nkongsamba, Aug. (fr), *Leeuwenberg 8153* (WAG); Mungo River valley between Ndo and gare de Mujuka, June (fr), *Fleury 33426* (P). **Centre Province:** hill Nkol Nlong, ca. 23 km W of Yaoundé, June (young fr), *Manning 2145* (MO); Son Mbong, ca. 50 km W of Eséka, Dec. (fr), *Bamps 1339* (BR, MO); 12 km W of Son Mbong, Mar. (fl bud & fl), *Leeuwenberg 5026* (BR, MO, WAG). **South Province:** Fifinda-Bella forest track 5 km E of Kribi-Edéa road, ca. 40 km N of Kribi, Feb. (fl & fr), *Bos 6259* (BR, P, WAG); 16 km E of Kribi, N of Lolodorf road, Sep. (fr), *Bos 5373* (BR, MO, WAG); Bipindi (fl bud), *Zenker 4913* (BM, BR, HBG, K, MO, S, W), (fl bud, fl & vegetative), *Zenker 4427* (BM, BR, HBG, S, W), (fl), *Zenker 4355* (BM, BR, HBG, K, MO, S, W); hill Nkolomeyan on road between Biwong Boulou and Koungoulou, 25 km SE of Ebolowa, Jan. (fl bud), *Letouzey 9839* (BR, HBG, P, WAG, YA); Meyo glem 9 km W of Sangmélima, Mar. (fl), *Meijer 15274* (MO); 10 km SW of Ambam, S of Ebolowa, Mar. (fl), *de Wilde & de Wilde-Duyfjes 2044* (BR, P, WAG); near Alati near Congo border SE of Djoum, Jan. (fl bud & fl), *Biholong 261* (BR, YA).

Pavetta staudtii is one of the most widespread species of subgenus *Baconia* in Cameroon, occurring in scattered locations in Southwest, Littoral, Centre, and South Provinces. It is centered in the Lower Guinea subcentre of specific endemism sensu White (1979) and is endemic to Cameroon, though it is predicted from collections near borders that range extensions will be discovered south and perhaps west of Cameroon.

Pavetta staudtii is in dense and open primary and secondary forest understory, mostly in high but not highest rainfall areas. It has been reported from elevations of 50–1100 m, usually from lowlands. Often collections have been reported to be sweet smelling. If a plant of subgenus *Baconia* has conspicuous and numerous punctate, subpunctate, or pustuliform black nodules mostly scattered on leaf blades, leaves often long compared to their width, and inflorescences always corymb- or subcorymb-shaped and usually neither large nor condensed, it is likely to belong to *P. staudtii*. South Province collections sometimes have more flowers and larger inflorescences than those from elsewhere.

Pavetta staudtii is distinct from *P. kribiensis*, which it resembles vegetatively, in having subquad-

rate (Fig. 5) rather than rotund to deltoid calyx lobes, less condensed inflorescences, and often fimbriate bracts.

27. Pavetta tenuissima S. D. Manning, sp. nov. TYPE: Cameroon. South Province: Ma'an, Nov. 1979 (fl), *Letouzey 15211* (holotype, P). Figure 23.

Frutices. Rami floriferi 0(sic facientes inflorescentias axillares)–10 cm. Folia costa et nervis secundariis subter prominentibus, nervis secundariis utroque 10–15; reticulo tenuissimo; venis tertiariis subter prominentibus. Inflorescentiae 0.5–2 cm latae, congestae, pubescentes. Lobi calycini triangulares ad rotundatos, ca. 0.5–1 × 1 mm, pubescentes saltem prope marginem. Corolla tubo 2–3 mm; lobis 2–4 mm, interdum super prope faucem pubescentibus. Styli exserti 2–3 mm.

Shrubs to 2 m. Twiglets pubescent, floriferous twiglets absent or to 10 cm. Leaves chartaceous, not or hardly anisophyllous, blades obovate (or less often elliptic), 14–31 × 6–11 cm, glabrous except margin sometimes pubescent; major veins below, costa and at times part of secondary veins above pubescent; apex acute to rounded, usually with acumen 3–20 × 3–10(–15) mm; base acute to obtuse (or occasionally rounded), sometimes asymmetrical; midrib and secondary veins prominent below, secondary veins 10–15 each side, usually joined 2–5 mm from margin; domatia absent or dense tufts of vestiture in branch vein angles of midrib and along secondary and tertiary veins below; nodules if present linear on side veins or of irregular shapes, scattered on blade; tertiary veins prominent below; fourth and higher order venation obvious above and below; venation density extremely fine. Stipules ± rotund or compressed rotund lobed, pubescent near base internally and densely pubescent or puberulent externally, awn linear, 5–9 mm. Inflorescences subumbellate or with subumbellate subunits, rotund in outline, 0.5–2 cm across, congested, sessile, pubescent, flowers (10–)50; sheathing bracts rotund lobed or unlobed and then saucer-shaped, pubescent externally, ± subglabrous internally, awns if present linear, 1–5 mm; other bracts ± subrotund to deltoid or linear, sometimes lobed, to 3 mm, not fimbriate, awn if present ca. 1 mm; bracteoles resembling smaller bracts. Calyx tube 0.2–0.8 mm long, 1–1.5 mm wide halfway up; lobes valvate, triangular or rotund, 0.5–1 × 1 mm, pubescent at least near margin, sometimes carinate, rim sometimes lighter. Corolla white or light green; tube cylindrical, 2–3 × 1 mm; lobes 2–4 mm, sometimes thinly pubescent above near throat. Style fusiform to clavate, pubescent, exserted 2–3 mm. Fruits ca. 5–10 mm across, glabrous to pubescent, bluish green. Mature seeds 2 or 1, attached ca. halfway up septum, concave.

Additional specimens examined. CAMEROON. **South Province:** Ma'an, Nov. (young fr & fr), *Letouzey 15217* (P, YA); Adjou, 17 km SE of Ambam, Mar. (fr), *Raynal & Raynal 10148* (P); Mékomengona, 17 km SW of Ambam, Feb. (fr), *Raynal & Raynal 9897* (P). **Littoral (Centre?) Province:** 50 km NW of Eséka, Kéllé River, Nov. (fr), *de Wilde & de Wilde-Duyfjes 1293* (WAG). **Southwest Province:** Banga, Southern Bakundu Forest Reserve, Mar. (young fr), *Brenan 9280* (K), *9280A* (K).

Pavetta tenuissima is only known from Cameroon, though three collections have been from South Province so close to the border with Rio Muni, Equatorial Guinea, that it probably exists there as well. It also occurs in southern Littoral (Centre?) and Southwest Provinces. It usually grows in wet lowland primary forest and has been reported from both riverine and transiently inundated forest and on clayish soil.

Pavetta tenuissima has the finest mesh reticulation of higher order leaf veins in Cameroon species of subgenus *Baconia.* The prominent, subrectangular gridlike pattern formed by the secondary and tertiary veins below is conspicuous to the naked eye, and distinctive. This subrectangular, gridlike venation also occurs in *P. muiriana*; these two species also have similar floral morphology. *Pavetta tenuissima* can be distinguished from *P. muiriana* by its extremely fine leaf vein reticulation, smaller and more congested inflorescences, mostly larger leaves, and smaller corollas.

Inflorescences of *Pavetta tenuissima* occasionally (*Raynal & Raynal 9897, de Wilde & de Wilde-Duyfjes 1293*) are on floriferous twiglets so reduced as to render them axillary. In this respect and in its condensed inflorescences, *P. tenuissima* resembles *P. camerounensis* subsp. *brevirama* and *P. grossissima.* The latter two taxa, however, do not have the extremely fine higher order leaf vein reticulation of *P. tenuissima,* which is so named because of this feature.

28. Pavetta urophylla Bremekamp, Bull. Jard. Bot. État 26: 257. 1956. TYPE: Zaïre. Équateur Province: km. 28–29 of road from Bikoro to Lac Tumba, May 1936 (fl), *Louis 1997* (holotype, U not seen; isotypes, BR, K).

KEY TO THE SUBSPECIES OF *PAVETTA UROPHYLLA*

1. Anthers septate, most calyx lobes ecarinate ..... subsp. *urophylla*
1. Anthers not septate, most calyx lobes carinate with carinae produced into apiculae ..... subsp. *bosii*

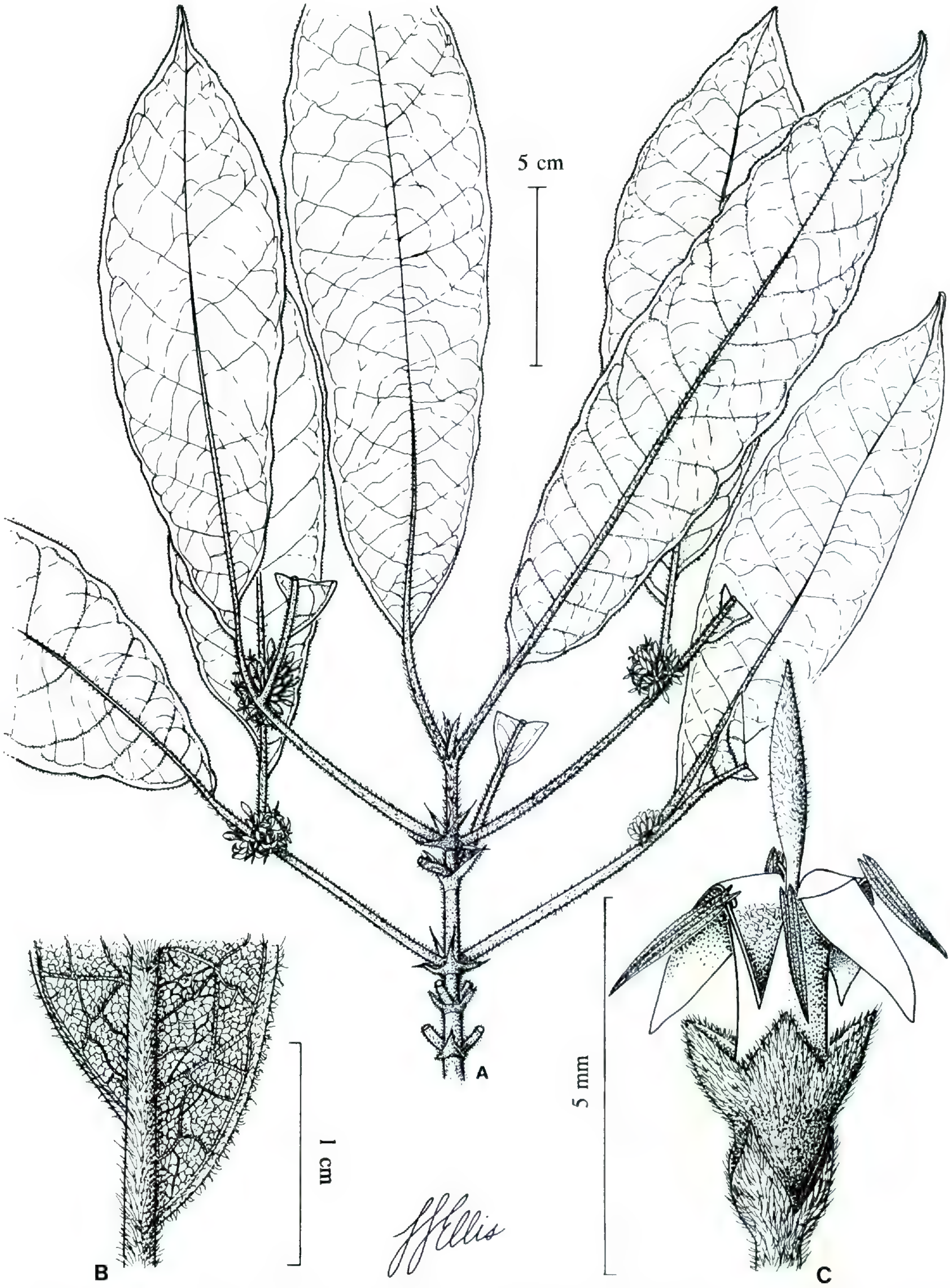


Figure 23. *Pavetta tenuissima* (*Letouzey 15211*, P).—A. Habit.—B. Lower surface of leaf base showing details of leaf venation, the finest seen in subgenus *Baconia*.—C. Flower.

a. Pavetta urophylla subsp. **urophylla**

Shrubs ca. 3 m. Twiglets glabrous, floriferous twiglets 6–24 cm. Leaves coriaceous, glabrous, sometimes anisophyllous; blades ovate to elliptical or oblong, sometimes asymmetrical, 5.5–29 × 2–11 cm; apex acute to obtuse, often asymmetrical, with acumen 10–45 × 3–12 mm; base cuneate to attenuate (or less often obtuse); midrib sometimes prominulous below, secondary veins (5–)10–14 each side, sometimes joined 3–5 mm from margin; mostly pubescent pocket domatia typically in most branch vein angles of midrib; nodules scattered on blade, usually conspicuous and more easily visible below; fourth and higher order venation obvious above and below; venation density fine. Stipules deciduous, rotund or deltoid lobed or unlobed and then cup-shaped, pubescent internally, glabrous externally, awn deciduous, the one seen cuspidate, ca. 1 mm. Inflorescences corymb-shaped, subcorymb-shaped, or pyramidal in outline, 2–7 cm across, ± lax, puberulent distally, subglabrous proximally, sessile, flowers 35–60(–100); sheathing bracts ovate lobed, deciduous, pubescent internally, glabrous externally, awns linear, 1–2 mm; other bracts obovate to linear, 0.2–2.5 mm, not normally fimbriate, sometimes with awn ca. 0.5 mm; bracteoles resembling smaller bracts sometimes present. Calyx tube 0.7–1 mm long, 1.5–2.5 mm wide halfway up; lobes valvate, subtruncate, ca. 0.1–0.5 × 1 mm, glabrous, usually ecarinate, drying brownish black, rim narrowly lighter. Corolla beige-tan; tube slightly broadening from base to throat, 2(–3.5) × 1–1.5 (–2.5) mm; lobes 4–5 mm, often thinly pubescent above near throat, reflexed. Anthers septate. Style fusiform, pubescent (to sometimes puberulent), exserted ca. 5–6 mm.

b. Pavetta urophylla subsp. **bosii** S. D. Manning, subsp. nov. TYPE: Cameroon. South Province: top of Calvary Mountain, 28 km ENE of Kribi, Lolodorf Road, Mar. 1970 (fl & young fr), *Bos 6611* (holotype, WAG). Figure 24.

A subspecie *urophylla* foliis valde discoloribus; inflorescentiis 3–5 mm pedunculatis; calyce lobis breviter triangularibus, denticulatis (ad interdum rotundato-compressos vel deltoideos), carinatis, carinis in apicula acuta productis; corolla lobis 2–4 mm; antheris nonseptatis differt.

Similar to subspecies *urophylla* except leaves more strongly discolorous; blades' venation density medium; inflorescences subglabrous distally, glabrous proximally, with peduncles to 5 mm with conspicuous ovate-lobed sheathing bracts at their bases and apices; bowl-shaped sheathing bracts also present distally on inflorescences; calyx tube sometimes only 0.5 × 1 mm, lobes short triangular, denticulate (or less often compressed rotund), with carinae produced into sharp apiculae, rim sometimes more broadly lighter; corolla brick red; anthers not septate; style puberulent to glabrous, exserted ca. 4–5 mm.

The most obvious features distinguishing subspecies *bosii* from subspecies *urophylla* are nonseptate anthers and apiculae on most calyx lobes. The more strongly discolorous leaves of subspecies *bosii* and the absence of extremely long acumens in subspecies *bosii*, such as sometimes occur in subspecies *urophylla*, are also noteworthy. Although the two subspecies could be considered separate species, this is not done because there are few collections and they clearly resemble each other more than either resembles any other known taxon.

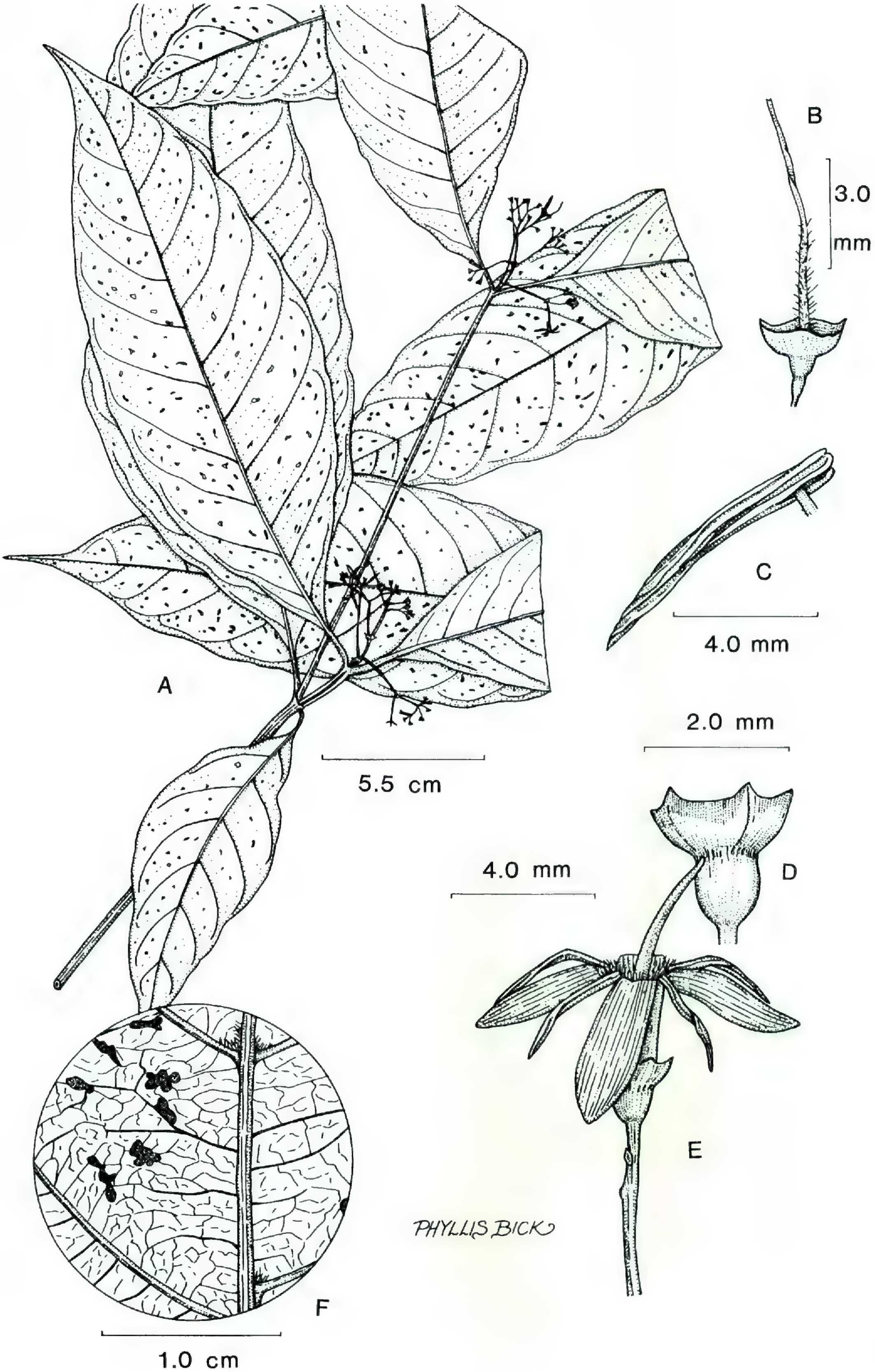
Subspecies *bosii* is known only from western South Province, Cameroon, in high forest, elevation unknown. Subspecies *urophylla* occurs in Zaïre and Congo. It has been collected at the edge of forest on sandy-clayey soil and in semideciduous, riverine, swampy, and seasonally inundated forests. Reported elevations from Zaïre are ca. 370 and 470 m.

Pavetta urophylla is one of the most distinctive species in subgenus *Baconia*. Distinguishing features are long leaf acumens, nodules more conspicuous from lower than upper leaf surfaces, brick red or beige-tan corollas, and calyx lobes often subtruncate near the base. Also, atypically in subgenus *Baconia*, the lower part of the style is not glabrous (Fig. 24).

29. Pavetta viridiloba K. Krause, Bot. Jahrb. Syst. 54: 353. 1917. TYPE: Cameroon. East Province: between Mpan (formerly Assobam) on Boumba River and Lomié, Apr. 1911 (fl), *Mildbraed 5120* (holotype, B destroyed; lectotype, selected here, HBG).

→

Figure 24. *Pavetta urophylla* subsp. *bosii* (*Bos 6611*, WAG).—A. Habit.—B. Flower, corolla removed to show style hairy below, glabrous further up, opposite of the normal situation in subgenus *Baconia*.—C. Anther.—D. Calyx.—E. Flower.—F. Part of lower leaf surface with domatia and bacterial nodules. Nodules in all other species of subgenus *Baconia* open toward the upper leaf surface.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B
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mm
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D
E
F
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PHYLLIS BICK

KEY TO THE VARIETIES OF *PAVETTA VIRIDILOBA*

1. Twiglets glabrous, leaf blades glabrous to subglabrous above, secondary veins only sparingly pubescent above (Fig. 25C) ..... var. *meurillonii*
1. Twiglets pubescent (to less often puberulent), leaf blades pubescent to subglabrous above, secondary veins densely pubescent above ..... var. *viridiloba*

a. Pavetta viridiloba var. **viridiloba**

Shrubs to 3 m. Twiglets pubescent (to less often puberulent), floriferous twiglets (6–)18–29 cm. Leaves chartaceous to coriaceous, sometimes anisophyllous; major veins pubescent, blades pubescent, sometimes thinly so, to subglabrous above, to puberulent below, obovate to elliptical, oblong (or less commonly ovate), 5–34 × 1.5–15.5 cm; apex obtuse to acute, subacuminate or with acumen 3–15 × 4–10 mm, acumen often at least as wide as long; base cuneate to attenuate, sometimes asymmetrical; midrib prominent below, secondary veins prominulous below especially toward base, 6–16 each side, eucamptodromous or brochidodromous; domatia absent except branch vein angles of midrib sometimes slightly indented or slightly more hairy than adjoining parts of veins; nodules absent, elongated along midrib or other veins, or scattered on blade; fourth and higher order venation usually obscure or invisible, usually slightly more easily visible below, visible on near-apical leaves on nonflowering shoot; venation density medium. Stipules deciduous, cup-shaped, pubescent internally and externally, awn linear to cuspidate, usually falcate, (<1–)1–9 × 1–2 mm. Inflorescences subcorymb-shaped to rotund or corymb-shaped in outline or with subunits of these shapes, 3–16 cm across, occasionally lax, pubescent, peduncle absent or to 8 mm; flowers 20–200, fragrant; sheathing bracts unlobed and cup- to saucer-shaped or subrotund to ovate lobed, pubescent internally, pubescent (to at times subglabrous with vestiture sometimes concentrated above subtending leaves) externally with awns resembling stipule awns 0.5–6 mm, linear awns 0.5–1 mm, or foliar appendages 2–7 mm; foliar bracts if present resembling but usually smaller than foliage leaves; other bracts ovate to linear, to 1.5 mm, sometimes with 1–several fimbriae 0.5–1 mm or fimbriae borne from axis directly; bracteoles resembling smaller bracts sometimes present. Calyx tube 1–1.5 mm long, 2.5–3.5 mm wide halfway up; lobes valvate, ovate to oblong, obovate, rotund, subquadrate or 2-lobulate owing to emarginate apex, 1.5–3 × 1–3.5 mm, pubescent, sometimes carinate, rim lighter. Corolla white; tube broadening from base to apex, 4–11 × (1–)1.5–3(–5) mm; lobes 5–8 mm. Style narrowly clavate, glabrous to puberulent, exserted 12–18 mm. Fruits ca. 5 mm across, subglobose or ellipsoid, thinly pubescent, pale gray. Seeds 1–2, attached ca. halfway up septum, concave, sometimes only shallowly so.

Additional specimens examined. CAMEROON. **East Province:** 9 km E of Lomié, Sep. (fr), *Leeuwenberg 6688* (WAG). **South Province:** Bitye, River Dja, Mar. (fl bud & fl), *Bates 1666* (BM, MO); between Dja River curve and Sangmélima, May (young fr), *Mildbraed 5468* (HBG); Ebemvok, 55 km W of Ebolowa, Mar. (fl bud and fl), *Raynal & Raynal 10432* (P, YA). **Centre Province:** 9 km E of Makak, June (young fr), *Manning 1970* (MO); 7 km ESE of Makak, June (young fr), *Manning 2037* (MO), *2095* (MO); 14 km SW of Yaoundé along new Yaoundé-Douala road, May (young fr), *Manning 1891* (MO).

b. Pavetta viridiloba var. **meurillonii** S. D. Manning, var. nov. TYPE: Cameroon. Southwest Province: Fontem, Mar. 1967 (fl bud), *Meurillon 617* (holotype, P). Figure 25.

A varietate *viridiloba* ramis glabris, foliis laminis super glabris vel subglabris, nervis secundariis super non nisi parce pubescentibus, inflorescentiis pubescentibus ad subglabras differt.

Similar to variety *viridiloba* except as in key to varieties. Also, pit domatia are occasionally present, the largest leaf seen has been 17 × 9 cm, and inflorescences can be partly subglabrous.

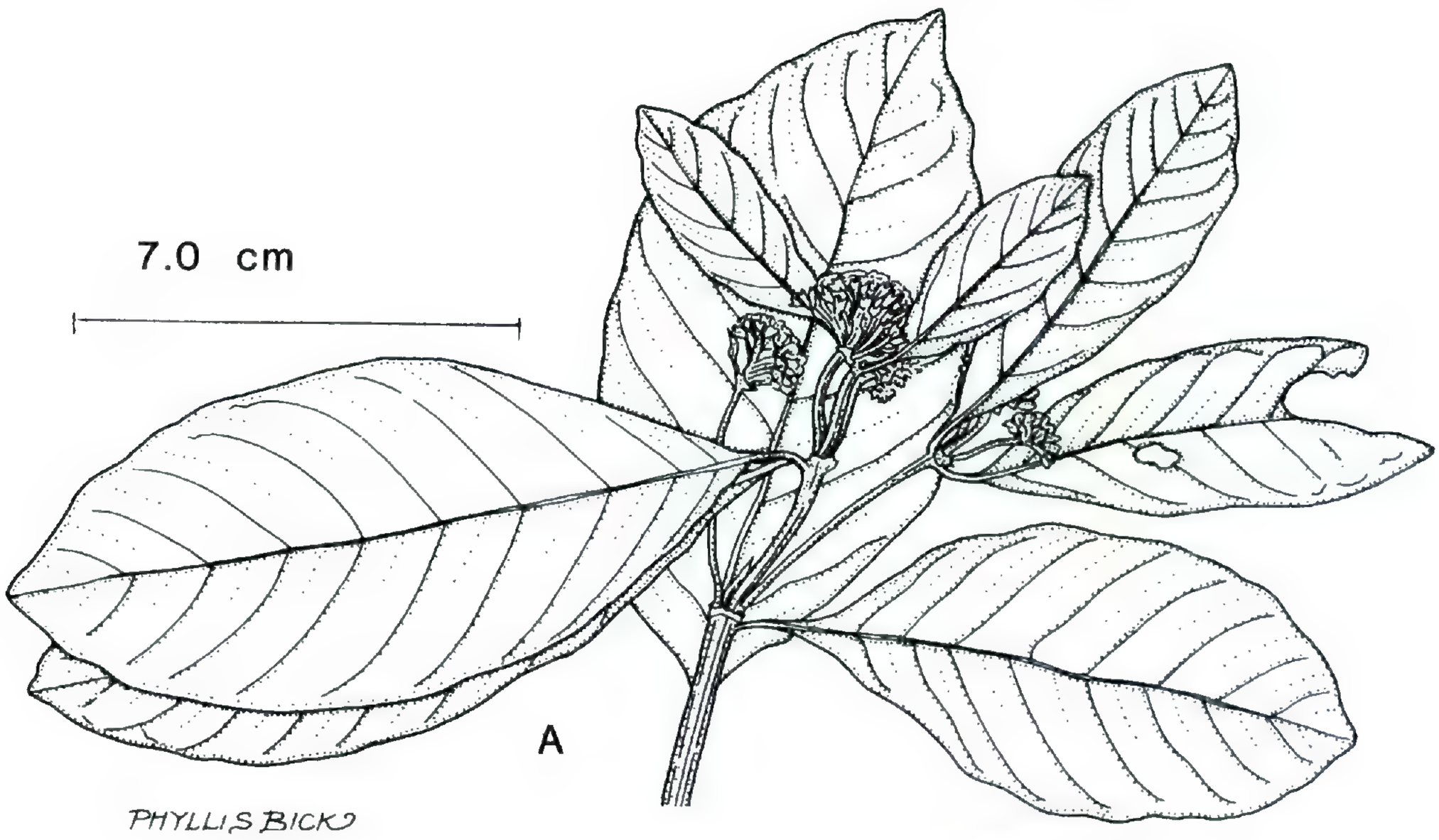
Variety *meurillonii* is recognized because, though it resembles variety *viridiloba* more closely than any other taxon, it is clearly different from all the collections of variety *viridiloba* in the features discussed above. It is also geographically distinct.

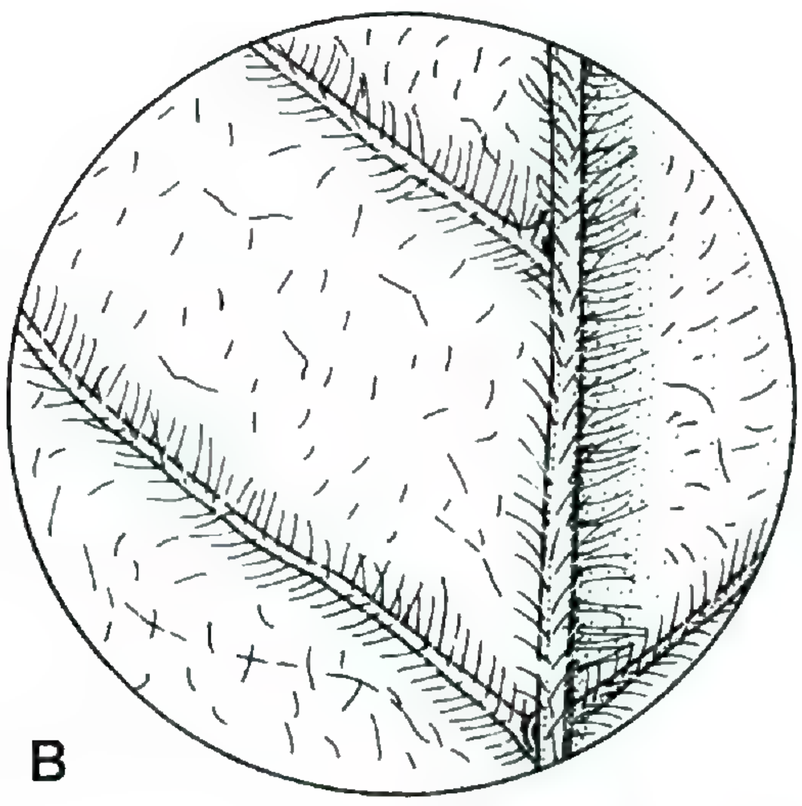
Variety *viridiloba* is endemic to south-central Cameroon, having been collected from South Province, southwestern East Province, and south-central Centre Province. Variety *meurillonii* is known only from the type from eastern Southwest Province, Cameroon.

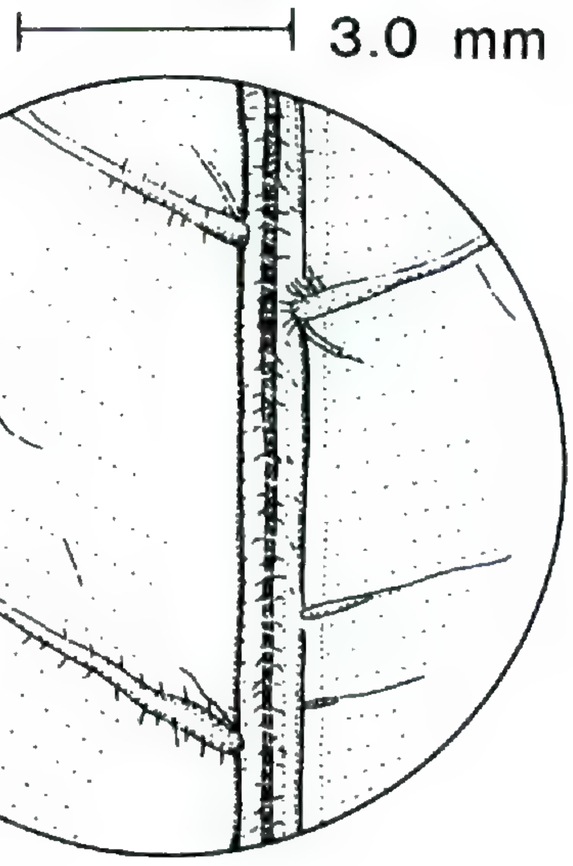
Pavetta viridiloba occurs in primary and secondary forest including disturbed forest, and in relatively open areas, at elevations of 600–1300 m.

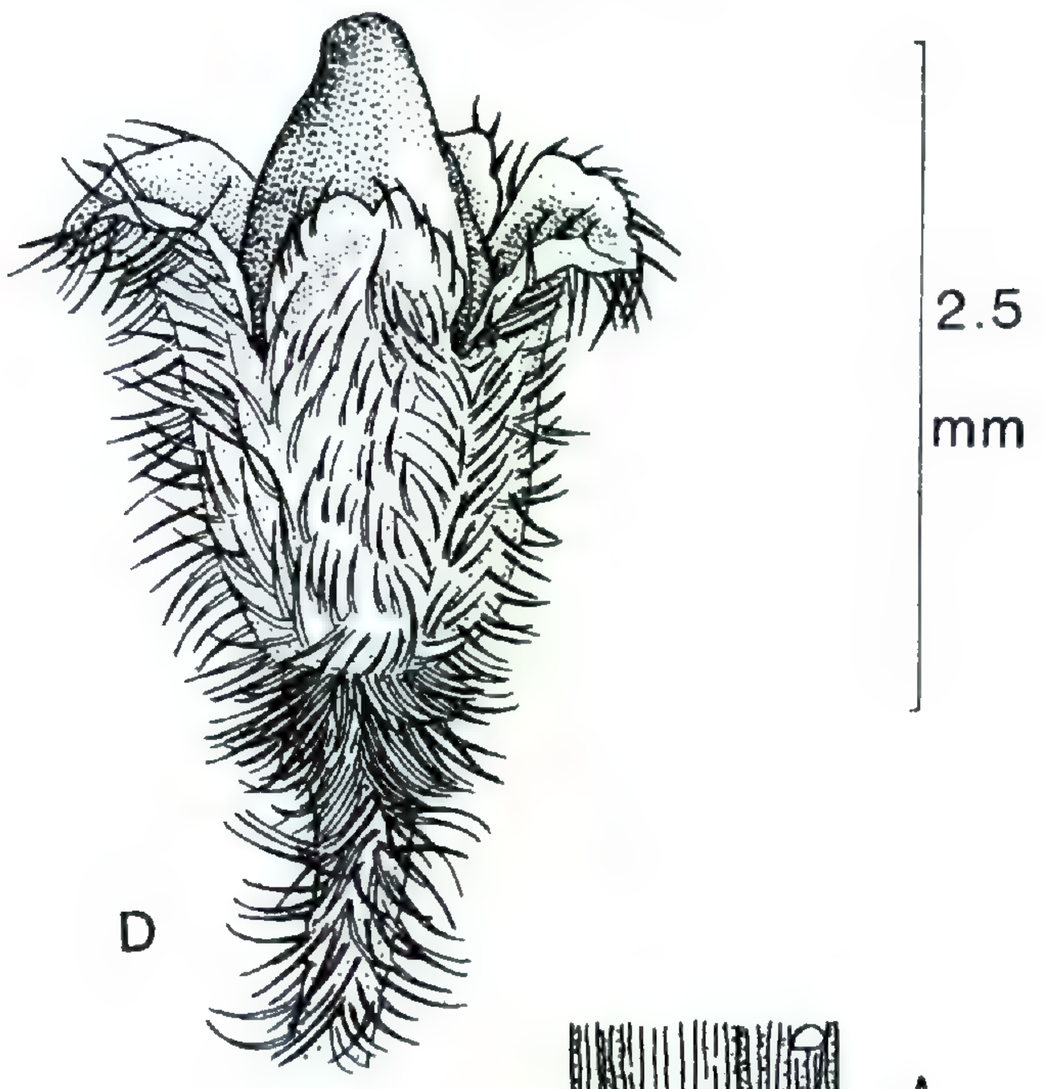
Bremekamp (1934) reduced *Pavetta viridiloba* to synonymy with *P. puberula*, but it is restored here. The two species can be distinguished in that calyx lobes are narrowly triangular with pointed tips in *P. puberula* but broadly ovate, oblong, or obovate or 2-lobulate (never with a pointed tip) in *P. viridiloba*. Further, there is almost always more vestiture in *P. viridiloba* than in *P. puberula*; calyx lobes are densely shaggily pubescent rather than only puberulent, and leaf blades are much more thickly pubescent.

Calyx lobes are usually green on herbarium sheets, accounting for the specific name, owing to vestiture thereon, a feature shared with *P. mpomii*.









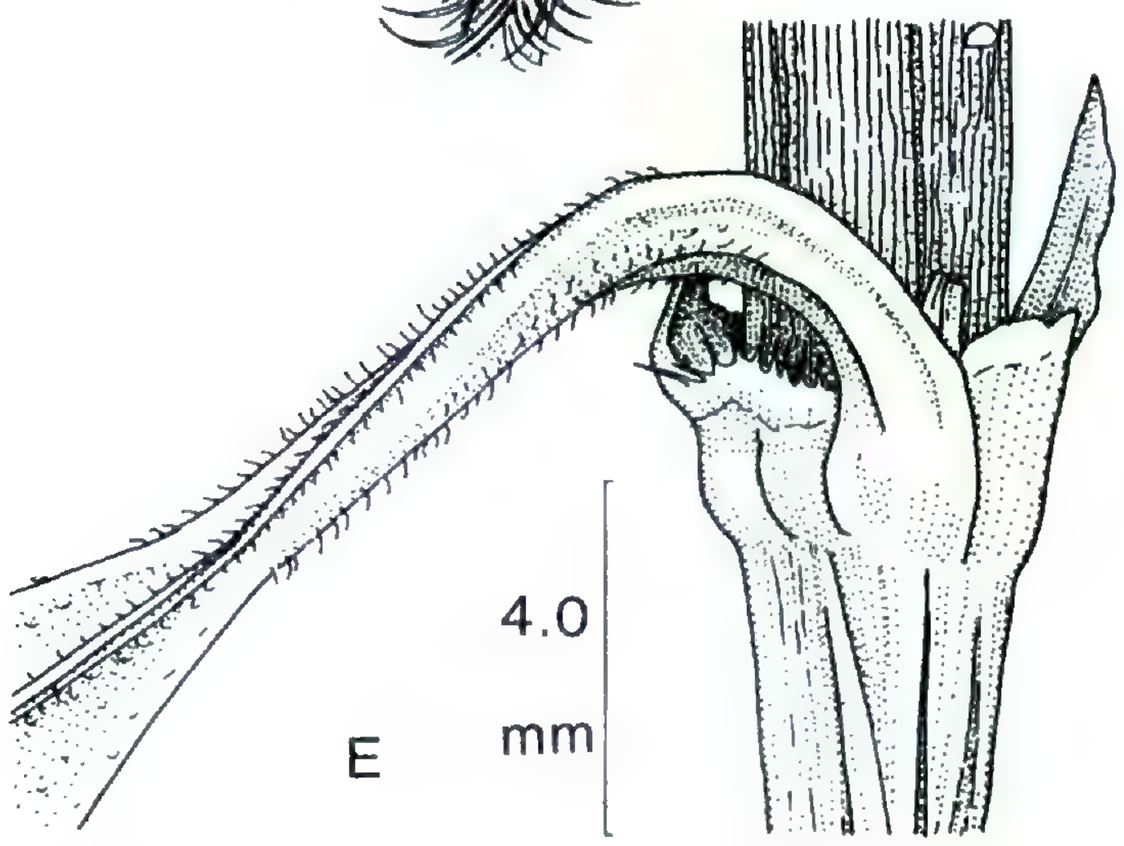


Figure 25. *Pavetta viridiloba* var. *meurillonii* (*Meurillon 617*, P).—A. Habit.—B. Part of lower leaf surface.—C. Part of upper leaf surface.—D. Flower bud.—E. Node and part of glabrous twiglet.

Calyces are usually longer and wider than those of most other taxa in subgenus *Baconia*. Leaf blades sometimes are among the largest in subgenus *Baconia*. They are olive green below.

Pavetta viridiloba can be distinguished from *P. mpomii* as in the key to species and as follows: some of its leaves reach a larger size than comparably placed ones in *P. mpomii*, floriferous twiglets are longer, most calyx lobes are more broadly elongate, corolla lobes are shorter, and styles are further exserted.

Occasional 5-merous flowers have been found in both varieties of *Pavetta viridiloba*.

The original species description did not indicate where the type was stored. *Mildbraed 5120* (B), seen by Bremekamp, is destroyed. *Mildbraed 5120* (HBG), the lectotype selected here, is the only duplicate of *Mildbraed 5120* found.

Taxon of Uncertain Status

Pavetta sp. near *brachycalyx*. *34593 HNC = SCA 1938* (YA) was collected from an unknown location probably in the Southwest Province of Cameroon and possibly cultivated in the Limbe Botanic Gardens without data. Although previously identified as *Pavetta corymbosa*, it is actually closer to *P. brachycalyx*. It differs from *P. brachycalyx* in having larger leaves and more flowers per inflorescence. Its origin is unknown and its status marginal either within *P. brachycalyx* or as a new species.

Cameroon Species Excluded from This Treatment

Pavetta bangweënsis Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 79. 1934. TYPE: Cameroon. East Province (probably): Bangwe (probably Bangué), *Conrau 66* (holotype, B destroyed).

No material fitting the description of this species has been found.

Species Not Known from Cameroon

Pavetta ankolensis Bridson, Kew Bull. 32: 610–612. 1978. TYPE: Uganda. *Eggeling 3709* (holotype, K; isotype, EA not seen).

Pavetta annobonensis Bremekamp, Repert. Spec. Nov. Regni Veg. 47: 16–17. 1939. TYPE: Equatorial Guinea. Pagalu Island, Sep. 1911, *Mildbraed 6676* (holotype, B destroyed; isotype, HBG).

Pavetta dermatophylla Mildbraed, Notizbl. Bot. Gart. Berlin-Dahlem 13: 704. 1937. TYPE: Equatorial Guinea. Pagalu Island, Sep. 1911, *Mildbraed 6749* (holotype, B destroyed; isotype, HBG).

Pavetta gossweileri Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 64. 1934. TYPE: Angola. Nov. 1911, *Gossweiler 5211* (holotype, BM).

Pavetta hymenophylla Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 68. 1934. TYPE: Tanzania. Lushoto District: Amani, Aug. 1911, *Grote 3541* (holotype, B destroyed; isotypes, EA not seen, K).

Pavetta dalei Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 72–73. 1934. TYPE: Kenya. Mt. Kenya, Oct. 1932, *Dale 3054* (holotype, K).

Pavetta intermedia Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 71. 1934. TYPE: Zaïre. Kivu Province: Lesse, Mar. 1914, *Bequaert 3136* (holotype, BR).

Pavetta ixorifolia Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 79. 1934. TYPE: Guinea. Fouta Djallon: Dalaba, Feb. 1907, *Caille 18137* (holotype, P).

Pavetta kasaica Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 69. 1934. TYPE: Zaïre. Kasai: Ipamu, June 1921, *Vanderyst 10774* (holotype, BR).

Pavetta micheliana J.-G. Adam, Bull. Inst. Fondam. Afrique Noire Sér. A, Sci. Nat. 35: 87–89. 1973. TYPE: Liberia. Mt. Nimba, Yiti valley, Jan. 1965, *Adam 20735* (holotype, P not seen; isotype, K).

Pavetta micrantha Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 74. 1934. TYPE: "Centralafrika" (Zaïre, Ituri?). Between Frumu and Mawambi, 1908, *Mildbraed 2908* (holotype, B destroyed; isotype, HBG).

Pavetta mollissima Hutch. & Dalziel, Fl. W. Trop. Africa 2: 91. 1931. TYPE: Ghana. 1929, *Vigne 1601* (holotype, K).

Pavetta monticola Hiern, Fl. Trop. Africa 3: 170. 1877. TYPE: São Tomé & Príncipe. São Tomé: *Mann 1074* (holotype, K; isotype, P).

Pavetta nitidula Hiern, Cat. African Pl. Collect. by Dr. Friedrich Welwitsch in 1853–61. Volume 1 part 2: 486. 1898. TYPE: Angola. Pungo Andongo, 1856–1857, *Welwitsch 3189* (holotype, BM).

Pavetta congensis Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 67. 1934. TYPE: Zaïre. Likimi, Feb. 1910, *Malchair 64* (holotype, BR).

Pavetta coriacea Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 69. 1934. TYPE: Uganda. Ruwenzori, Nov. 1893, *Scott Elliot 8310* (holotype, K).

Pavetta obanica Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 77. 1934. TYPE: Nigeria. Oban, 1911, *Talbot 359* (holotype, BM).

Pavetta oblongifolia Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 65. 1934. TYPE: Sénégambia. 1838, *Heudelot 673* (holotype, K; isotypes, BM, W).

Pavetta oresitropha Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 73. 1934. TYPE: Equatorial Guinea. Bioko Island, Nov. 1911, *Mildbraed 7135* (holotype, B destroyed; isotype, HBG).

Pavetta polyantra Bremekamp, Repert. Spec. Nov. Regni Veg. 47: 21. 1939. TYPE: Gabon. Upper Ogowé: Lastoursville, Oct. 1929, *Le Testu 7541* (holotype, Herb. Le Testu = BM, isotypes, BR, P).

Pavetta puberula Hiern, Fl. Trop. Africa 3: 171. 1877. TYPE: Gabon. Sierra del Crystal, July 1862, *Mann 1718* (holotype, K).

Pavetta redheadii Bremekamp, Repert. Spec. Nov. Regni Veg. 47: 18. 1939. TYPE: Zambia. Mwinilunga, Nov. 1937, *Milne-Redhead 3429* (holotype, K; isotype, BR).

Pavetta schweinfurthii Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 66. 1934. TYPE: "Central Africa" (Sudan?). Gr. Seriba Ghaddar, Apr. 1869, *Schweinfurth 1341* (holotype, K).

Pavetta ternifolia (Hooker f.) Hiern, Fl. Trop. Africa 3: 177. 1877. TYPE: Tanzania. Bukoba District: Karangwe, Feb. 1862, *Speke & Grant 422* (holotype, K).

Pavetta yalaënsis Bremekamp, Kew Bull. 8: 501. 1954. TYPE: Kenya. Nandi District: Kaimosi, N of Yala River, May 1933 or 1951, *Rogers 741* (holotype, K marked 1933; isotypes, BM marked 1933, BR marked 1951, EA not seen, S marked 1951).

Pavetta urundensis Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 66–67. 1934. TYPE: "West Urundi" (Burundi?). *Meyer 1037* (holotype, B destroyed).

Pavetta virungensis Bremekamp, Bull. Jard. Bot. État 14: 307–309. 1937. TYPE: Zaïre. Kivu: Virungu Mountains, Karisimbi volcano, Feb. 1932, *Lebrun 4952* (holotype, BR).

Pavetta vanderijstii Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 68. 1934. TYPE: Zaïre? Kikveil (= Kikwit?), Oct. 1920, *Vanderyst 8133* (holotype, BR).

Pavetta yambatensis Bremekamp, Repert. Spec. Nov. Regni Veg. 37: 74. 1934. TYPE: Zaïre(?). Yambata, Feb. 1914, *De Giorgi 1718* (holotype, BR; isotype, K).

Pavetta zimmermanniana Valeton, Icon. Bogor. 2, Fasc. 3 tab 143. 1904. TYPE: Indonesia, Cultivated in *Bogor Botanic Garden* as #*603*, origin uncertain, not seen.

The "South Cameroons, Gaboon River" specimen of this species, *Mann 961* (K), is from present-day Gabon rather than Cameroon.

Species Not Known from Cameroon Originally Described in but Subsequently Excluded from *Pavetta* Subg. *Baconia*

Tarenna funebris (Bremek.) N. Hallé, Adansonia 7: 505. 1967. *Pavetta funebris* Bremek., Repert. Spec. Nov. Regni Veg. 37: 63. 1934. TYPE: Zaïre. Kasai: Mpio-mpio, Aug. 1921, *Vanderyst 10221* (holotype, BR).

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Erratum

Baldwin, Bruce G., Michael J. Sanderson, J. Mark Porter, Martin F. Wojciechowski, Christopher S. Campbell & Michael J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: A valuable source of evidence on angiosperm phylogeny. Ann. Missouri Bot. Gard. 82: 247–277.

An error in the original of Figure 4 in this article has been discovered by the authors.

Base 1 of the hypothetical ITS 2 secondary structure in Figure 4 is the last base at the 3′ end of the 5.8S subunit ("C," position 424 in Baldwin, 1993) adjacent to ITS 2. The numerical designation of each of the variable ITS 2 base positions in Figure 4 should be increased by one (e.g., 19 becomes 20, 25 becomes 26, etc.) and the indicated locations of the variable sites should be shifted two bases forward throughout the diagram. Sites 28, 76, 104, and 176 (designated as 27, 75, 103, and 175 in Fig. 4) should not be indicated as variable. Site 95 should be indicated on the diagram as a variable site (one change, in *C. hooveri*). The adjustments in positioning of variable sites results in a shift from six pairs to only two pairs of changes that map to directly opposing sites along a stem (sites 20 and 37 and sites 26 and 33). Based on the ITS phylogeny of *Calycadenia*, changes at each of the two pairs of sites were independent, unlinked events that occurred in different lineages and do not represent examples of compensatory change to maintain ITS 2 secondary structure. The above corrections do not impact the conclusions about evolution of ITS 2 secondary structure presented in the paper.

Volume 83, Number 1, pp. 1–152 of the Annals of the Missouri Botanical Garden was published on 25 January 1996.

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Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin.*" Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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Cover illustration. *Pavetta camerounensis* subsp. *camerounensis* S. D. Manning, sp. nov., by Linda Ellis.

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The Annals, published quarterly, contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden, St. Louis. Papers originating outside the Garden will also be accepted. Authors should write the Managing Editor for information concerning arrangements for publishing in the ANNALS. Instructions to Authors are printed in the back of the last issue of each volume.

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A REVISION OF *DISCOCARPUS* (EUPHORBIACEAE)[1]

Sheila M. Hayden and W. John Hayden[2]

Abstract

As revised here, *Discocarpus* is interpreted to consist of three neotropical species: *D. essequeboensis* Klotzsch, *D. gentryi* S. M. Hayden, which is described and named herein as new to science, and *D. spruceanus* Müll. Arg. One previously accepted name, *D. brasiliensis* Klotzsch ex Müll. Arg., is reduced to synonymy of *D. essequeboensis*. Lectotypes are proposed for the two species previously described. One species is newly excluded from *Discocarpus*, as are three others, following previous literature. Foliar anatomy is described with a focus on epidermal sclereids, which are shown to occur on both epidermides. Evidence presented supports close relationships with *Lachnostylis* Turcz. and *Amanoa* Aubl.; little was found to support previous hypotheses concerning a relationship with *Chonocentrum* Pierre ex Pax & K. Hoffm.

Discocarpus Klotzsch is a genus of trees found in seasonally flooded riparian habitats of northern South America, where they are components of the forest canopy. The plants are dioecious and bear small clusters of flowers in the axils of simple, alternate, entire leaves.

Discocarpus was first described by Klotzsch (1841) who initially named, but did not describe, two species; he subsequently described one of these, *D. essequeboensis* Klotzsch (1843), based on Schomburgk collections from the Essequibo River region of Guayana. Omitting two nettles (Urticaceae) from Mexico and Nicaragua grossly misplaced in the genus, the next species of *Discocarpus* to be named was *D. spruceanus* Müll. Arg. (1863), based on collections of Richard Spruce from the Rio Negro of Brazil. Some 32 years after being first mentioned by Klotzsch, *D. brasiliensis* Müll. Arg. (1873) was formally named, based on a collection of von Martius from the early 19th century. Three taxa were added to the genus in the 20th century. The first addition was *D. hirtus* (L. f.) Pax & K. Hoffm. (Pax & Hoffmann, 1922), a consequence of synonymizing the South African genus *Lachnostylis* with *Discocarpus*. In current literature, however, *Lachnostylis* is treated as distinct from *Discocarpus* (e.g., Levin, 1986; Mennega, 1987; Webster, 1994b). The two most recently described species,

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D. mazarunensis Croizat (1948) and *D. duckeanus* Jabl. (1967), were based on South American material.

Jablonski (1967) accepted the five South American species noted above as distinct entities constituting *Discocarpus*, but his treatment indicated several gaps in the available data on these plants. For example, staminate or pistillate flowers were undescribed for several species. Furthermore, recent studies reveal that two of the species accepted by Jablonski were misplaced in *Discocarpus*, and presently available collections indicate the existence of a previously unrecognized species (Hayden, 1995). In addition, the issue of generic relationships is unresolved. *Discocarpus* was classified most recently in subfamily Phyllanthoideae Asch. tribe Wielandieae Baill. ex Hurus. (Webster, 1994b), but earlier concepts of generic relationships have varied widely (see below). Moreover, reports of foliar sclereids in *Discocarpus* and *Amanoa* (Gaucher, 1902; Levin, 1986) suggest the new possibility of placement in tribe Amanoeae. This paper provides a revision of *Discocarpus*, including detailed descriptions of foliar anatomy and discussion of relationships.

Materials and Methods

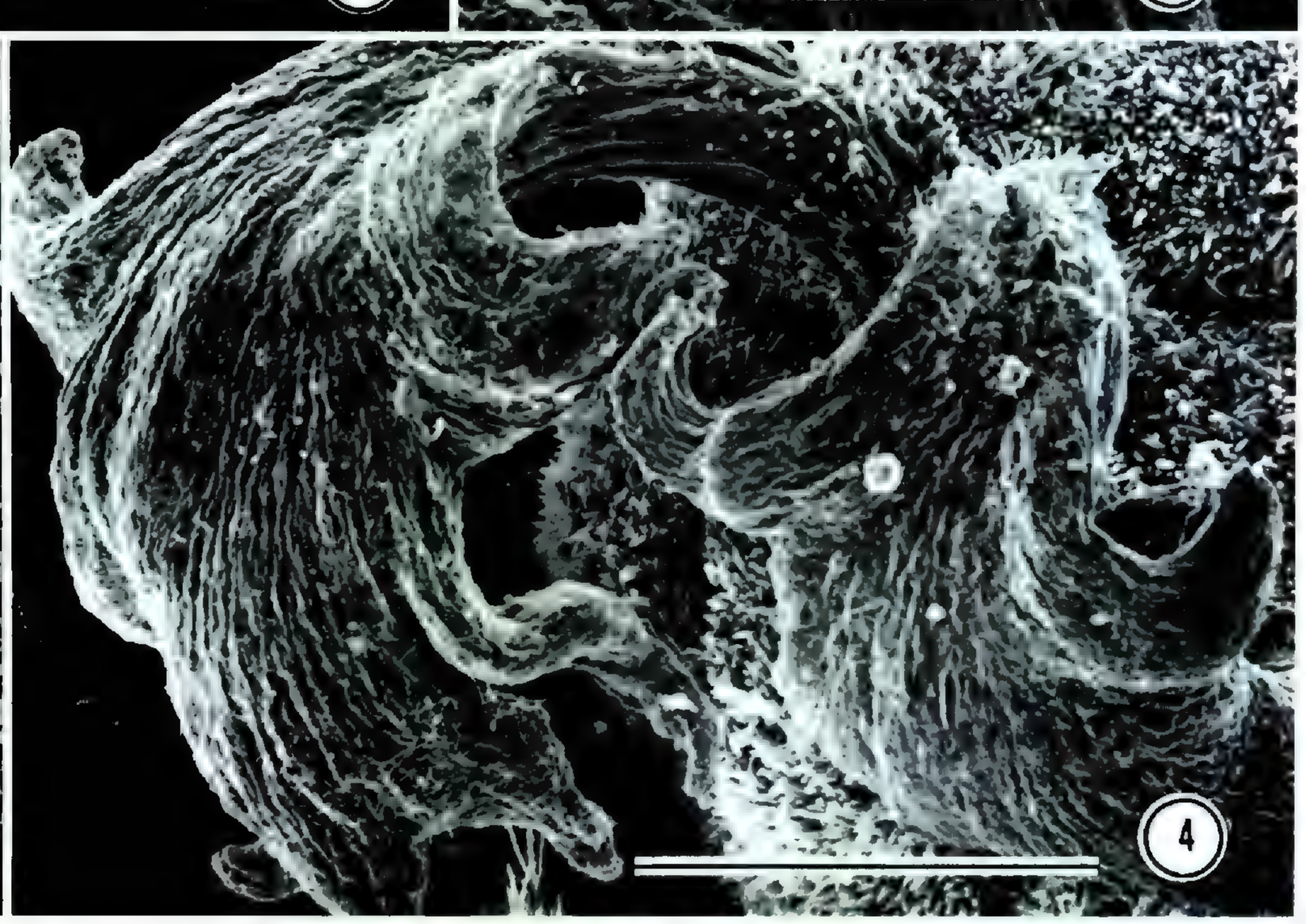
This revision is based on a total of 171 herbarium specimens of *Discocarpus* borrowed from 29 herbaria in the United States, Europe, and South America. Small samples of leaf tissue from the following collections were removed for anatomical study: *Discocarpus essequeboensis* Klotzsch, *Jangoux & Bahia 294* (NY), *Krukoff & Fróes 11974* (NY), *Maas et al. 7395* (U), *Schomburgk 659* (U), *Silva 4776* (NY), *Smith 2692* (F); *Discocarpus gentryi* S. M. Hayden, *Encarnación 25065* (F), *Vázquez & Jaramillo 5487* (NY); *Discocarpus spruceanus* Müll. Arg., *Davidse 27631* (NY), *Wurdack & Adderly 43349* (NY). Half of each sample was mounted directly on stubs and sputter coated with a gold/palladium mixture prior to observation with SEM. The second half of each sample was rehydrated by boiling in water with a few drops of Aerosol OT, dehydrated in tertiary butanol, embedded in paraffin, and sectioned at 10 μm on a rotary microtome. Paraffin sections were stained in toluidine blue (Berlyn & Miksche, 1976) or a combination of saffranin and haematoxylin (Johansen, 1940).

Systematic Treatment

Discocarpus Klotzsch, Archiv. Naturg. 7(1): 201. 1841. TYPE: *Discocarpus essequeboensis* Klotzsch. Figures 1–4.

Dioecious trees (or shrubs), (3–)10–30 m tall, DBH 25–100 cm. Twigs glabrous to short-pilose, silvery gray to dark purplish red; lenticels raised, elongate, parallel with the axis; terminal buds acuminate, cylindric, glabrous to tomentose, 3–7 mm long, often with two basal knoblike protrusions, sometimes sexually dimorphic. Leaves alternate, simple, petiolate, glabrous, leathery; petioles 4–8 mm long, wrinkled; margins entire; base obtuse; apex acute to acuminate; venation pinnate; ultimate veins reticulate, orthogonal. Stipules fugaceous. Inflorescence axillary, 1–several flowers per node; flower clusters sessile, subtended by cupulate bracts; bracts ca. 1 mm long, 1 mm wide, glabrous to pubescent; staminate clusters several per node; pistillate clusters one per node. Staminate flowers sessile, congested, 10–30 per node; sepals (4) 5, 1.5–2 mm long, 1–1.5 mm wide, pilose; petals (0–)5, delicate, hyaline, glabrous to pubescent, less than 1 mm long, linear, often fringed apically; disk extrastaminal, lobed; stamens (4) 5; filaments fused below the level of the disk, free portions 1.5–3 mm long; anthers elongate, 1 mm long, longitudinally dehiscent, exserted; pistillode segmented into two or three linear, pubescent, membranous filaments. Pistillate flowers 1–3(–5) per node; pedicels essentially lacking to 5 mm long; sepals 5, cupulate, 1.5–3 mm long, 1–2 mm wide, densely pubescent; petals (0–)5, hyaline, 0.5–3 mm long, up to 1 mm wide, pubescent; disk slightly lobed; ovary 3-carpellate, subglobose, smooth or sculpted, densely pubescent; styles 3, parted to the base or nearly so, spreading horizontally, densely pubescent below; stigmas 3, dilated, lobed, horizontal or reflexed; ovules 2 per locule. Fruits symmetrically 3-lobed or asymmetrically subglobose, 6–12 mm tall, 6–15 mm diam., longitudinally dehiscent into 2, 3, or 6 mericarps, 1–3-seeded; pericarp ca. 1 mm thick, hard, brittle; surface smooth to deeply sculpted, densely pubescent; columella persistent. Seeds subglobose, ecarunculate; testa thin, shiny.

Discocarpus can be distinguished from other woody genera of subfamily Phyllanthoideae by the combination of: deciduous stipules; dioecy; minute petal-bearing flowers produced in axillary clusters; lobed extrastaminal disks; finely reticulate exine on pollen grains; and styles that are not bifid, but terminate in three dilated, irregularly lobed stigmas. It is noteworthy that floral merosity and presence of petals are somewhat inconstant. Most flowers are 5-merous, but 4-merous flowers are not infrequently encountered. Most flowers examined showed petals to be present and isomerous with the sepals, but sometimes fewer petals, or even none, will be



Figures 1–4. Floral morphology of *Discocarpus*, SEM. 1, 2, *Discocarpus spruceanus* Müll. Arg., *Spruce 3527* (G). —1. Staminate flower with sepals and petals removed to show fused filaments; bar = 1 mm. —2. Fused filaments; bar = 250 μm. —3. *Discocarpus essequeboensis* Klotzsch, *Martius s.n.* (L). Hair on fruit surface; bar = 250 μm. —4. *Discocarpus essequeboensis* Klotzsch, *Schomburgk 35* (G). Dilated, lobed, reflexed stigmas; bar = 1 mm.

found. Notably, the minute size and flimsy texture of the petals render them easy to overlook. Important clues to recognizing the genus in sterile condition include the elongate terminal buds with paired distinctive basal knobs and fine veins forming highly regular minute areoles that lack free-ending veinlets.

In Webster's (1994b) key to genera of Wielandieae, two aspects of morphology of staminate flowers attributed to *Discocarpus* are at variance with

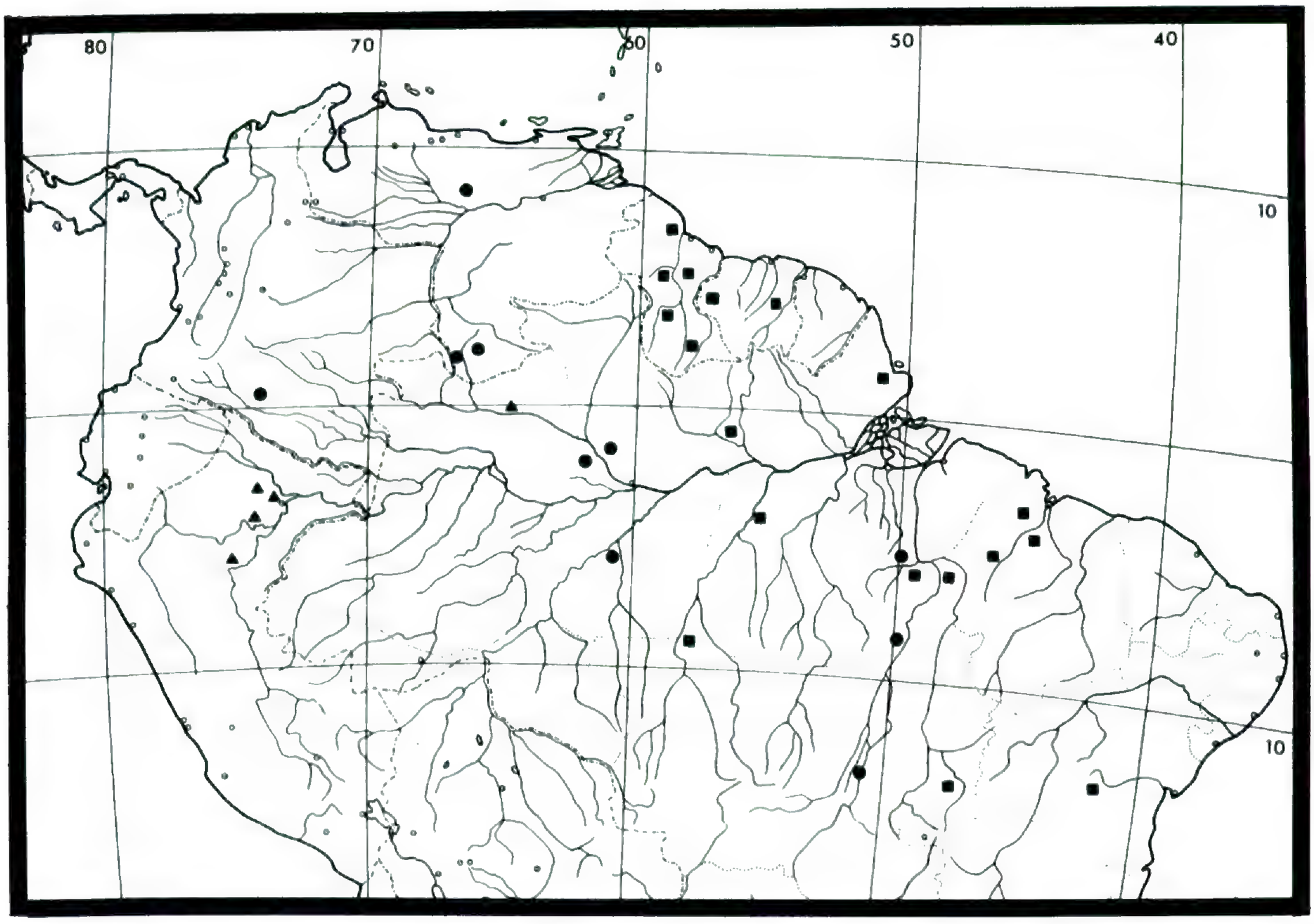


Figure 5. Distribution of *Discocarpus*. Squares = *Discocarpus essequeboensis* Klotzsch; circles = *Discocarpus spruceanus* Müll. Arg.; triangles = *Discocarpus gentryi* S. M. Hayden.

the above description. Staminate flowers are sessile and bear filaments fused to the base of the pistillode, features also noted by Pax and Hoffmann (1922).

Three species of *Discocarpus* occur in the Amazon and Orinoco River basins of Brazil, Colombia, Peru, and Venezuela, as well as smaller rivers of Guyana and Surinam (Fig. 5). Habitat is lowland rainforest below 250 m, along seasonally flooded riverbanks of *várzea* forests or occasionally inundated fields. *Discocarpus* species can form canopy trees, but samples are sometimes collected from specimens described as small shrubs.

KEY TO SPECIES OF *DISCOCARPUS* (FIGS. 6–9)

1a. Terminal bud of staminate specimens lacking basal knobs, covered with dense indumentum; ovary and fruit surface smooth; fruits 1(–2)-seeded, 2 carpels usually abortive; widely scattered in the Amazon and Orinoco River basins ..... *D. spruceanus* Müll. Arg.

1b. Terminal bud of staminate specimens with two prominent basal knobs, glabrous or only sparsely pubescent; ovary and fruit surface sculpted; fruits 3-seeded, all carpels accrescent.

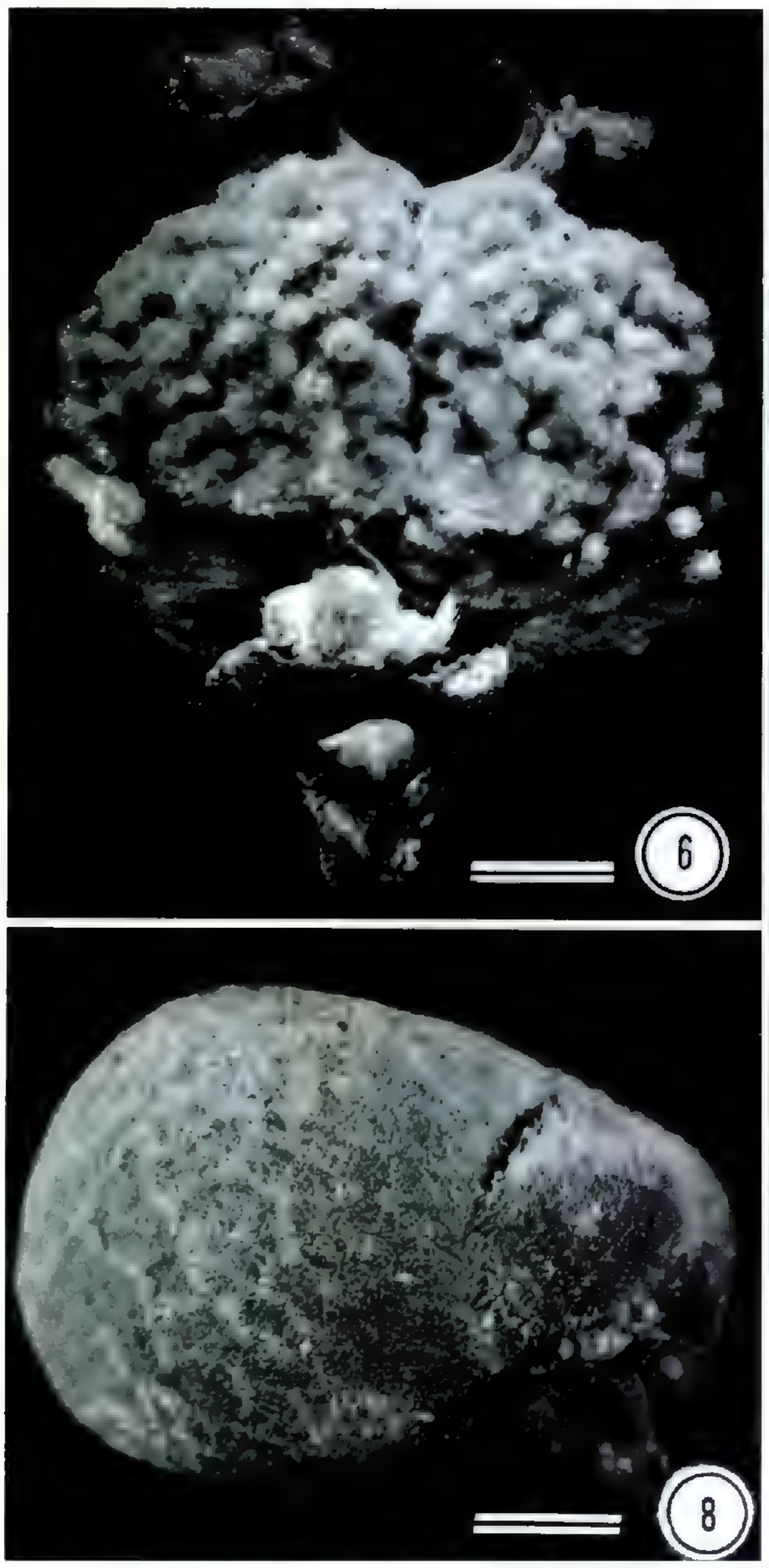
2a. Pistillate flowers on pedicels 4–5 mm long; ovary and fruit surface deeply sculpted into long undulate ridges with sharp crests (beneath dense indumentum); fresh staminate flowers yellow; Amazonian Peru and western Brazil ..... *D. gentryi* S. M. Hayden

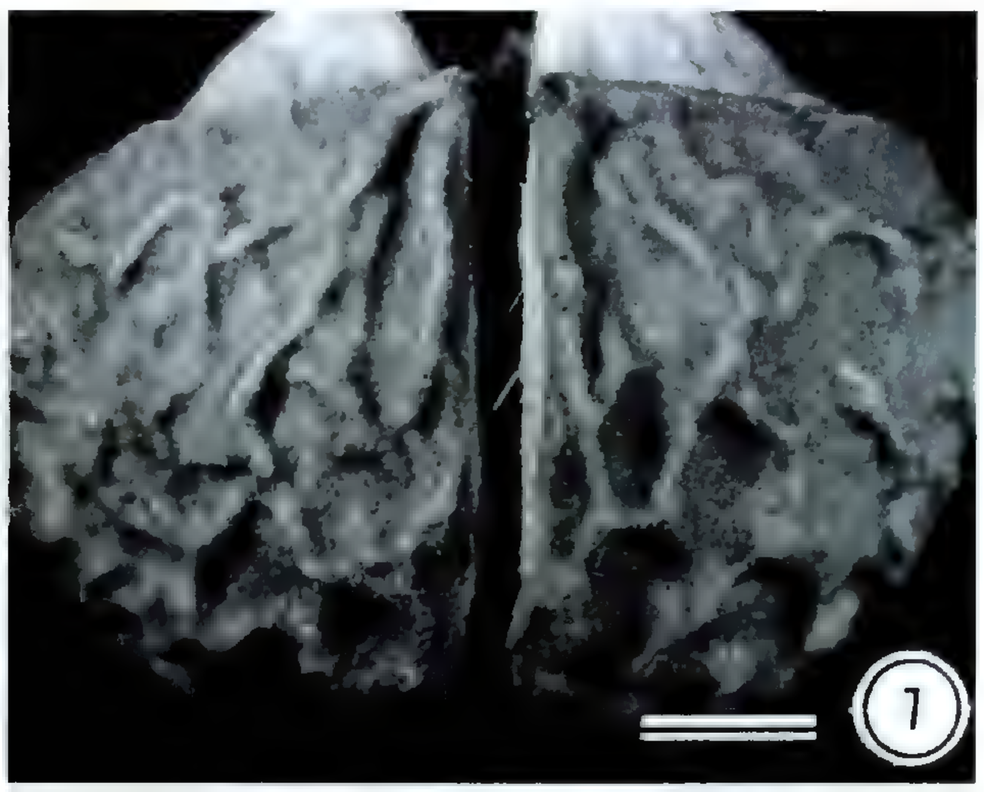
2b. Pistillate flowers sessile or nearly so; ovary and fruit surface weakly sculpted into muricae or short undulate ridges with rounded crests (beneath dense indumentum); fresh staminate flowers cream; Guyana, Surinam, and northeastern Brazil ..... *D. essequeboensis* Klotzsch

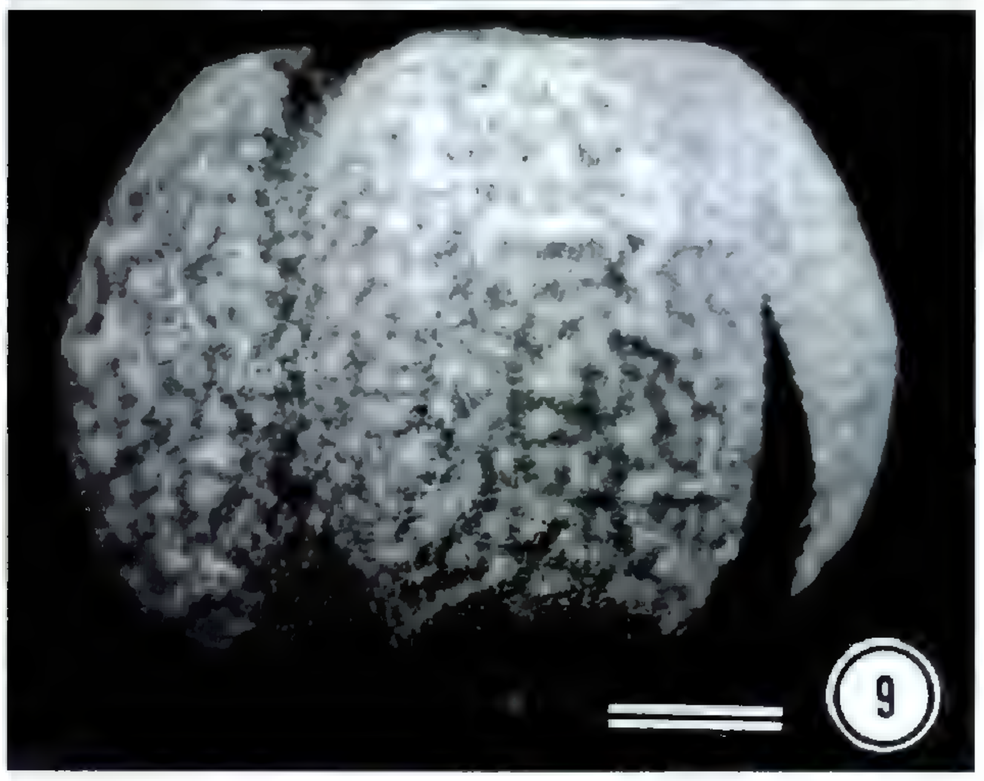
Discocarpus essequeboensis Klotzsch, London J. Bot. 2: 52. 1843. TYPE: Guyana. On branch of upper Essequibo River, *Schomburgk 35* (lectotype, selected here, BM; isolectotypes, G, K, OXF, P, U, W). Figures 10, 3, 4, 9.

Discocarpus brasiliensis Klotzsch ex Müll. Arg. Mart. Fl. Bras. 11(2), 13: 1873. SYNTYPES: Brazil. Bahia: near Villa do Rio de Contas, *Martius s.n.* (G, L, M, MO); Bahia: *Martius s.n.* (M).

Trees, 10–20 m tall, DBH 25–100 cm. Terminal buds similar in staminate and pistillate specimens, glabrous, with two basal knobs. Leaves 8–22 cm long, 4–8 cm wide; apex acuminate (to 10 mm long) to merely acute. Inflorescence bracts glabrous to pubescent. Staminate flowers 10–30 per node,







Figures 6–9. Ovary and fruit surface features of *Discocarpus*. —6. *Discocarpus gentryi* S. M. Hayden, *Gentry et al. 18419* (F). Ovary. —7. *Discocarpus gentryi* S. M. Hayden, *Revilla 411* (NY). Mature fruit. —8. *Discocarpus spruceanus* Müll. Arg., *Spruce 3527* (P). Mature fruit with one developed and two aborted lobes. —9. *Discocarpus essequeboensis* Klotzsch, *Schomburgk 706* (G). Mature fruit. All bars = 2 mm.

cream-colored; sepals (4) 5, 2 mm long, 1.5 mm wide; petals (0–)5, pubescent; disk lobed; stamens (4) 5; pistillode segments 3. Pistillate flowers 1–5 per node; pedicel 0–1 mm; sepals 3 mm long, 2 mm wide, light green; petals reduced, (0–)5, 0.5–3 mm long; ovary shallowly muricate to reticulate; stigmas reflexed. Immature fruits dark red; mature fruit brown, symmetrically 3-lobed, 8–9 mm tall, 10–15 mm diam., 3-seeded, surface weakly sculpted into shallow muricae or short undulate ridges with rounded crests. Seed 6–8 mm diam.; micropylar and basal surfaces somewhat flattened; testa red-brown.

Distribution. Central and eastern Brazil, Guyana, Surinam (Fig. 5); on sandy soil in frequently inundated forest along rivers (*várzea*) and periodically flooded fields. Flowers have been collected from June through December; fruits, from September through December.

Common Names. "Square Wood" (in reference to shape of trunk, *Anderson 408*); "Oity do Campo" (*Fróes & Krukoff 11974*).

Additional specimens examined. BRAZIL. **Amapá:** *Bastos 201* (MO). **Amazonas:** *Martius s.n.* (L); Maués, *Pires 109* (NY, U). **Bahia:** Villa do Rio de Contas, *Martius s.n.* (G, L, M). **Goiás:** Rio Araguaia at mouth of Rio Javaés, *Silva 4862* (ILLS, NY); Rio Piranha, *Silva 4776* (NY). **Maranhão:** Rio Alto Turiaçu, Nova Esperança, 2°5'S, 45°5'W, *Jangoux & Bahia 294* (NY, RB); Rio Pindare Basin, Monçao, *Fróes & Krukoff 11974* (GH, MICH, NY, US); Rio Mearim-Lapela, municipality de Vitória do mearim, Campo Coberto, *Silva 4191* (RB). **Mato Grosso:** margin of Rio Juruena, *Rosa & Santos 2149* (MO, NY). **Pará:** Marabá, *Fróes & Black 24336* (P, U); Cachoeira Porteria, Rio Trombetas, *Ducke 8953* (BM, G); Rio Trombetas margin, *Ducke 7988* (BM); Rio Trombetas margin,

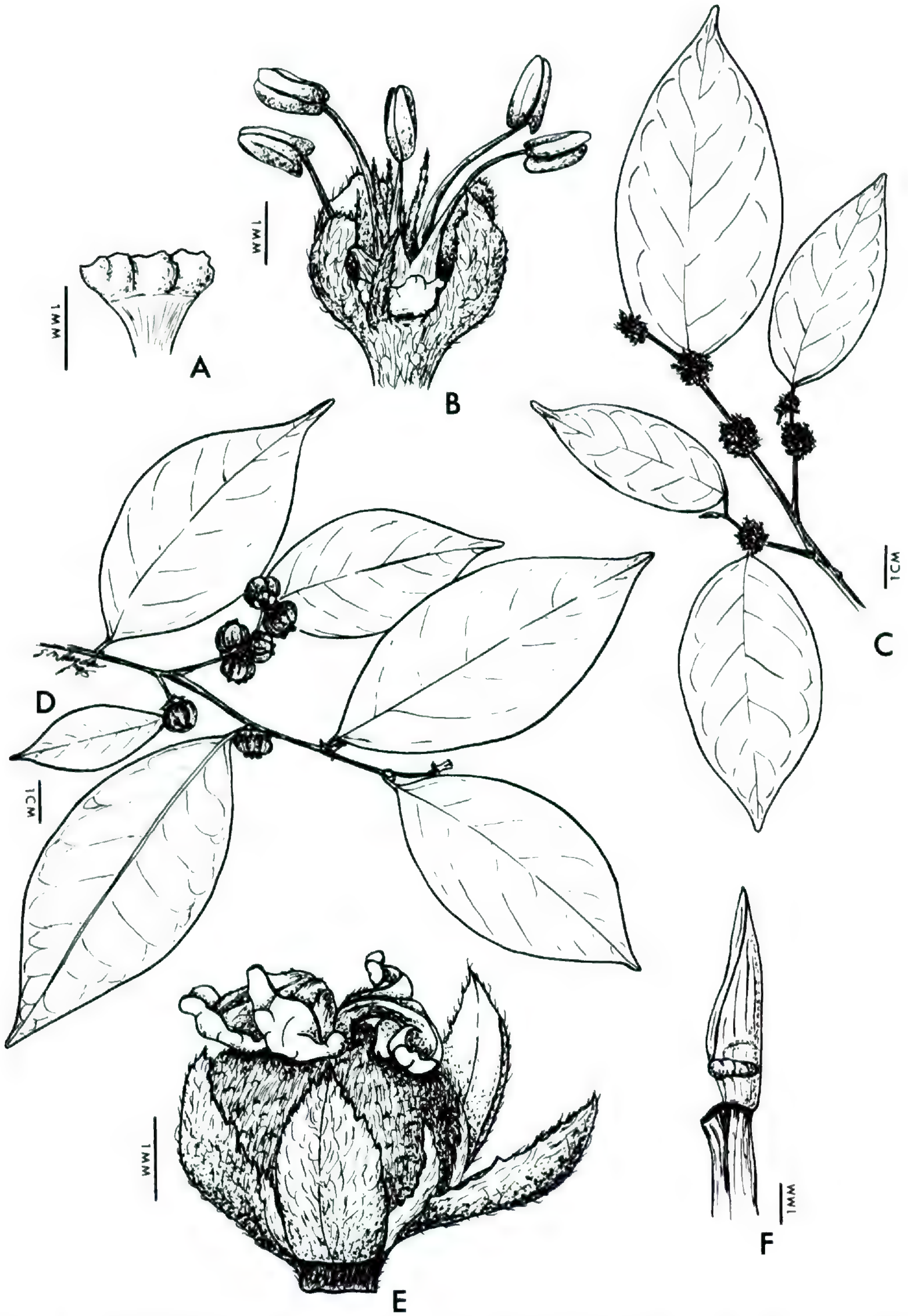


Figure 10. *Discocarpus essequeboensis* Klotzsch. —A. Disk from staminate flower; *Pires 109* (U). —B. Staminate flower, one sepal removed; *Pires 109* (U). —C. Habit, staminate specimen; *Krukoff 11974* (NY). —D. Habit, pistillate specimen; *Rosa & Santos 2149* (MO). —E. Immature fruit; *Schomburgk 35* (W). —F. Terminal bud; *Krukoff 11974* (NY).

Ducke 7993 (BM); National park of Tapajós, 60 km from Itaituba-Jacarecanga at the margin of Rio Tapajós, *Silva & Rosário 3992* (NY). GUYANA. Upper Essequibo River, *Schomburgk 706* (BM, G, K, L, P, U, W); upper Essequibo River, *Schomburgk 659* (BM, E, F, G, K, L, MANCH, OXF, P, U, W); Rupununi Savanna, near Maricouba pond near Karanambo Ranch, 3°45′N, 59°19′W, *Görts-van Rijn et al. 388* (URV); Rupununi District, Kuyuwini Landing, Kuyuwini River, forest along river, 2°5′N, 59°15′W, *Jansen-Jacobs et al. 2903* (URV); Manakobi, Courantyne River, *Anderson 408* (K), *Schomburgk s.n.* (L, U), *Schomburgk 1237* (F), *Schomburgk 920* (F, G, K, P, W); Cuyuni-Mazaruni Region, Essequibo River 6–8 km downstream of Omai, 5°26′N, 58°42′W, *Gillespie 1573* (MO); Rupununi River, Monkey Pond landing SW of Mt. Makarapan, 3°53′N, 58°55′W, *Maas et al. 7395* (P, U); basin of Essequibo River near mouth of Onoro Creek, 1°35′N, *Smith 2692* (F, G, NY). SURINAM. Matappi, Corantÿne, *B. W. 2044* (U); Tapanahoni, *Kappler 97* (L, U, W), *Kappler 2143* (GOET, W), *Schomburgk 459* (G).

Notes. Klotzsch's species *Discocarpus essequeboensis* was originally based upon three collections, *Schomburgk 35* (pistillate flowers), *Schomburgk 659* (staminate flowers), and *Schomburgk 706* (mature fruits). Since staminate material of *Discocarpus* reveals few diagnostic characters, and since the fruiting specimen bears only fragmentary label data, the pistillate collection, *Schomburgk 35*, is by far the best choice to typify the species. The BM specimen includes abundant flowers that prove important in defining the species (see below). The spelling of the specific epithet adopted here follows that used by Klotzsch (1843) in contrast to that of the earlier nomen nudum, *Discocarpus essequiboensis* Klotzsch (Archiv. Naturg. 7(1): 201. 1841).

Discocarpus brasiliensis is here placed in synonymy under *Discocarpus essequeboensis*. The two entities are virtually indistinguishable, and it seems that recent practice has been to identify material from the Guianas as *D. essequeboensis* and Brazilian specimens as *D. brasiliensis*. In the past, *Discocarpus brasiliensis* was supposedly distinguished from *D. essequeboensis* by the presence of small bumps or muricae on ovaries and fruits of the former in contrast to the smooth ovaries and fruits of the latter (Müller, 1873; Pax & Hoffmann, 1922). However, the syntypes of *D. essequeboensis* listed by Klotzsch include a fruiting specimen, *Schomburgk 706*, which has a surface texture that is obviously bumpy and identical to other specimens identified as *D. brasiliensis*. Further, the lectotype of *Discocarpus essequeboensis*, *Schomburgk 35*, illustrates a range of developmental stages from very young flowers just emerging from the bud to early fruits. The flowers on this specimen reveal a developmental change in ovary surface from nearly smooth to contoured or bumpy as the ovary matures. On the basis of these observations, and given the lack of any other consistent character of either pistillate or staminate material of *D. essequeboensis* and *D. brasiliensis* that delineates two separate species, the decision was made to place *Discocarpus brasiliensis* in synonymy under *Discocarpus essequeboensis*. Both names were first published by Klotzsch; however, the name *D. brasiliensis*, published in 1841, remained a *nomen nudum* until Müller provided it with a diagnosis in 1873. Thus *D. essequeboensis*, published in 1843, is the oldest legitimate name for this species.

In addition to those named *Discocarpus brasiliensis* Klotzsch, other specimens collected by Martius bear the name *D. bahiensis* Klotzsch, but it appears that the latter name has never been published. It is noteworthy that, aside from these nearly 200-year-old collections by Martius, no other collections of *Discocarpus* have been seen from the Atlantic coastal forest of Brazil.

Discocarpus gentryi S. M. Hayden, sp. nov. TYPE: Peru. Loreto: Santa María de Nanay, SW of Río Nanay, *Schunke V. 2443* (holotype, F; isotypes, G, GH, NY, US). Figures 11, 6, 7.

Arbor vel frutex dioecia, 3–14 m; gemma terminalis glabra; flores staminati lutei; flores pistillati 1 (2) per nodum; pedicellus florum pistillatorum 4–5 mm longus; fructus trilobus symmetricus, seminibus tribus; pericarpium undulatum profunde, viride; testa cinnamomea.

Trees or shrubs, 3–14 m tall, DBH 35–40 cm. Terminal buds similar in staminate and pistillate specimens, glabrous to sparsely pubescent, with two basal knobs. Leaves 7–15 cm long, 3–7 cm wide; apex acute to acuminate. Inflorescence bracts glabrous to somewhat pubescent apically. Staminate flowers 15–30 per node, bright yellow; sepals 2 mm long, 1 mm wide; petals (0–)5, glabrous to sparsely pubescent; disk with fingerlike lobes; stamens 5; pistillode segments 2–3. Pistillate flowers 1 (2) per node; pedicels 4–5 mm long; sepals 3 mm long, 2 mm wide; petals 5, 2 mm long, 1 mm wide; ovary surface deeply undulate; stigmas reflexed. Fruit green, symmetrically 3-lobed, 12 mm tall, 15 mm diam., 3-seeded, surface deeply sculpted into long undulate ridges with sharp crests. Seeds ca. 8 mm diam.; micropylar and basal surfaces somewhat flattened; testa golden brown.

Distribution. Amazonian Peru and western Brazil (Fig. 5); on white sand or clay soil of low, seasonally inundated forest along rivers (*várzea* or *tahuampa*); 120–150 m altitude. Flowers have been collected from December through April; fruits, from September through February.

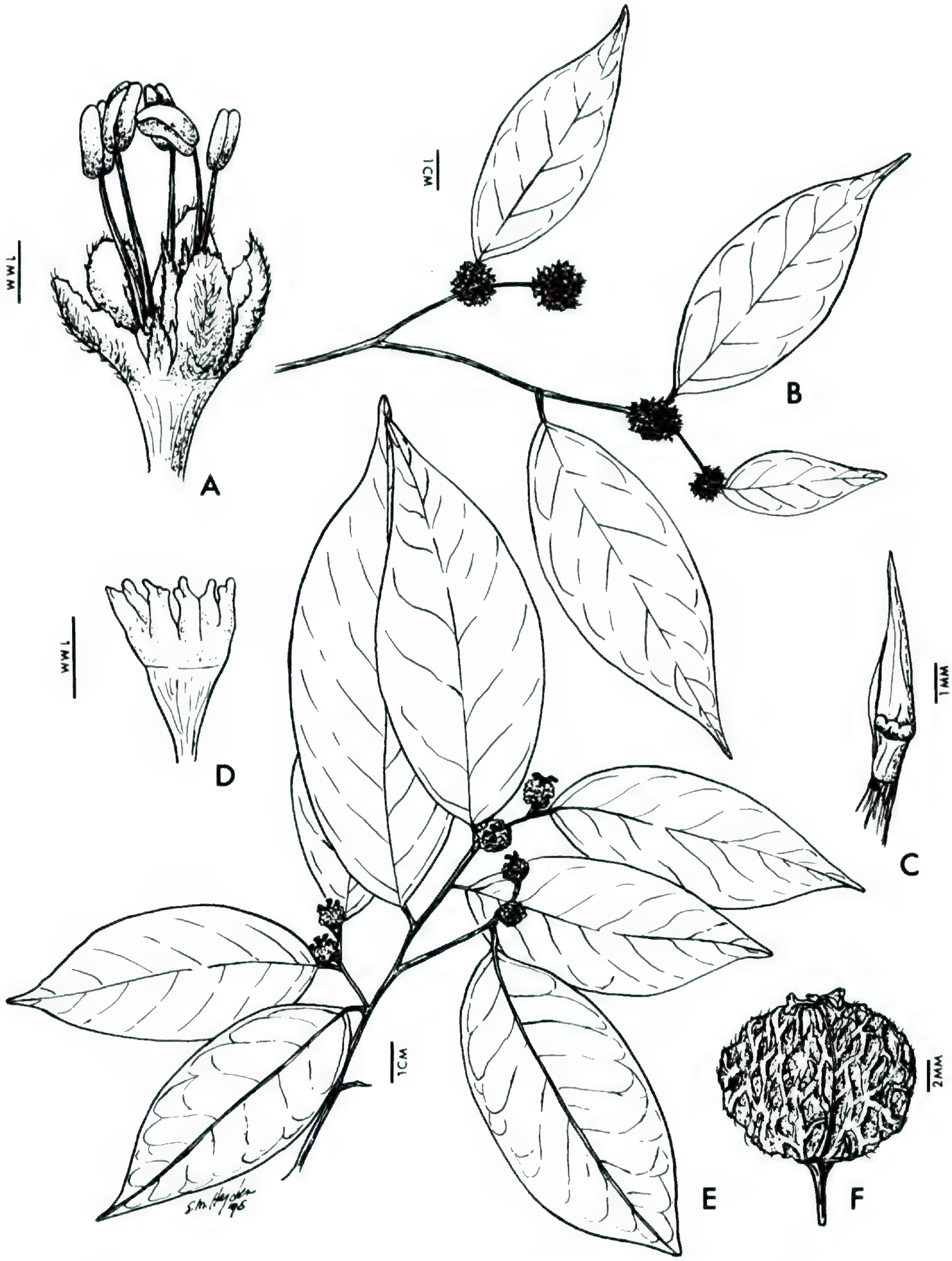


Figure 11. *Discocarpus gentryi* S. M. Hayden. —A. Staminate flower; *Rimachi Y. 3300* (NY). —B. Habit, staminate specimen; *Rimachi Y. 3300* (MO). —C. Terminal bud; *Rimachi Y. 3300* (MO). —D. Disk from staminate flower; *Rimachi Y. 3300* (NY). —E. Habit, pistillate specimen; *Gentry et al. 18419* (F). —F. Fruit; *Revilla 411* (F).

Common Names. "Ucuchahuasi" (*Vásquez & Jaramillo 5487*); "Loromicuna" (*Ayala 1415*).

Additional specimens examined. BRAZIL. **Amazonas:** Rio Negro near Ilha Provedençia, *Steward et al. 516* (NY). PERU. **Loreto:** Maynas, Iquitos, Río Nanay, Quebrada de Morropon, *Rimachi Y. 3281* (F, MO, NY, RSA); Río Nanay, 03°51′S, 73°32′W, *Vásquez et al. 7528* (F, NY); Río Nanay at Almendras, 03°48′S, 73°25′W, *Vásquez & Jaramillo 5487* (F, MO, NY); Iquitos, in the gorge of the small settlement of San Pablo de Cuyana above Santa Clara de Nanay, *Rimachi Y. 3300* (F, MO, NY, RSA); Caño Iricahua, below Jenuro Herrera, on the left margin of Río Ucayali, *Encarnación 25065* (F); Iquitos, Río Nanay, 8 bends in the river above de Morona Cocha, *Revilla 411* (F, MO, NY); vicinity of Iquitos, *Revilla 3598* (F, MO); Río Itaya below San Juan de Muniches, 40 mins. above Iquitos with 40 hp motor, *Gentry et al. 18419* (F, MO); right margin of Zungarococha, primary forest, *Ayala 1415* (MO).

Notes. Peruvian specimens of *Discocarpus* referred here to *D. gentryi* have only been collected within the last 30 years. The genus was not treated in MacBride's (1951) earlier compilation of Euphorbiaceae for the *Flora of Peru,* although the presence of *D. brasiliensis* was predicted. When specimens from Peru with sculpted fruit surfaces first came to light they were identified as *D. brasiliensis,* and they are referred to as such in Brako and Zarucchi's (1993) checklist. However, *D. brasiliensis* is herein synonymized with *D. essequeboensis,* and, further, the Peruvian collections prove to be distinct both morphologically and geographically from this species. As noted in the key, fruits of *D. gentryi* have pronounced surface relief, and pistillate flowers are distinctly pedicellate. In contrast, fruits of *D. essequeboensis,* though somewhat sculpted, are smoother, and pistillate flowers are sessile or nearly so. Additionally, mature capsules of *D. essequeboensis* are brown and the seeds are dark brown, in contrast to the mature capsules of *D. gentryi,* which are green and contain golden brown seeds. Careful dissection of staminate flowers of *D. gentryi* reveals disk lobes much more elongate than those of the other two species. *Discocarpus gentryi* has been collected most frequently along riverbanks near Iquitos, Peru, especially in the vicinity of Río Nanay, a blackwater river. There is one additional record of the species from western Brazil, along the Rio Negro, another blackwater river.

The specific epithet commemorates Alwyn H. Gentry (1945–1993), for his many important contributions to the floristics of Central America and northern South America. Gentry's collection of *Discocarpus* from the region around Iquitos, Peru, was instrumental in recognizing these plants as new to science.

Discocarpus spruceanus Müll. Arg., Linnaea 32: 78. 1863. TYPE: Brazil. Amazonas: Rio Negro above the mouth of the Casiquiare River, *Spruce 3527* (lectotype, selected here, BM; isolectotypes, BR, C, E, F, G, GH, GOET, K, LD, MO, NY, OXF, P, TCD, W). Figures 12, 1, 2, 8.

Drypetes krukovii Monach., Phytologia 3: 34. 1948. TYPE: Brazil. Amazonas: Municipality Humayta, near Livramento, on Rio Livramento, *Krukoff 6703* (holotype, NY; isotypes, G, US).

Trees, 10–30 m tall, DBH 30–60 cm. Terminal buds sexually dimorphic, densely pubescent with very small to no basal knobs in staminate trees, usually glabrous to sparsely puberulent and with two basal knobs in pistillate trees. Leaves 5–12 cm long, 2–5 cm wide; apex acute to acuminate. Inflorescence bracts pubescent. Staminate flowers 15–30 per node, pale yellow; sepals 4–5, 1.5 mm long, 1 mm wide, pubescent; petals 4–5, glabrous to sparsely pubescent; disk irregularly lobed; stamens 4–5; pistillode segments 2–3. Pistillate flowers 1–3 per node; pedicels 1–5 mm long; sepals 1.5 mm long, 1 mm wide; petals 5, 1.5 mm long, 0.5 mm wide; ovary smooth; stigmas horizontal. Fruit brown, subglobose, asymmetrically 3-lobed by abortion of 2 (1) carpels, 6–9 mm tall, 6–7 mm diam., 1(–2)-seeded, surface smooth. Seed shape and dimensions unknown (usually shriveled in herbarium specimens); testa brown.

Distribution. Widely scattered in the Amazon and Orinoco River basins of Brazil, Colombia, and Venezuela (Fig. 5); in *várzea* or *rebalse* vegetation of frequently inundated forest along rivers; often locally abundant. Flowers have been collected from January through August; fruits, in November and December.

Additional specimens examined. BRAZIL. **Amazonas:** Rio Negro, northern Brazil, *Spruce 3781* pro parte (BM, BR, C, E, F, G, GH, GOET, K, MO, NY, OXF, TCD, W); Airão, *Ducke 904* (F, MO, NY, R, UC, US). **Mato Grosso:** proximity of Rio Cristalino, 13°13′S, 50°51′W, *Dovebroś* (RB). **Pará:** Rio Itacaiuna, cachoeira Grande, *Fróes & Black 24513* (U); proximity of Conceição do Araguaia, 8°44′S, 49°26′W, *Mileski 120* (RB). COLOMBIA. **Caquetá:** 2 km S of Solano, 8 km SE of Tres Esquinas on Río Caquetá below mouth of Río Ortequaza, *Little & Little 9604* (US). VENEZUELA. **Amazonas:** Río Guainia between Comunidad and Santa Rita, *Wurdack & Adderley, 43349* (NY, S, US); Caño Adobo, 25 km S of San Cargos of Río Negro, 1°38′N, 66°58′W, *Liesner 8634* (MO, NY); Departamento Río Negro, lower part of the Río Baria, 1°27′–1°10′N, 66°32′–66°25′W, *Davidse 27631* (F, MICH, MO, NY); Departamento Atabapo, Riverina del Caño Yagua, 03°37′N, 66°35′W, *Marin 479* (MO).

The syntype collections of *Discocarpus spru-*

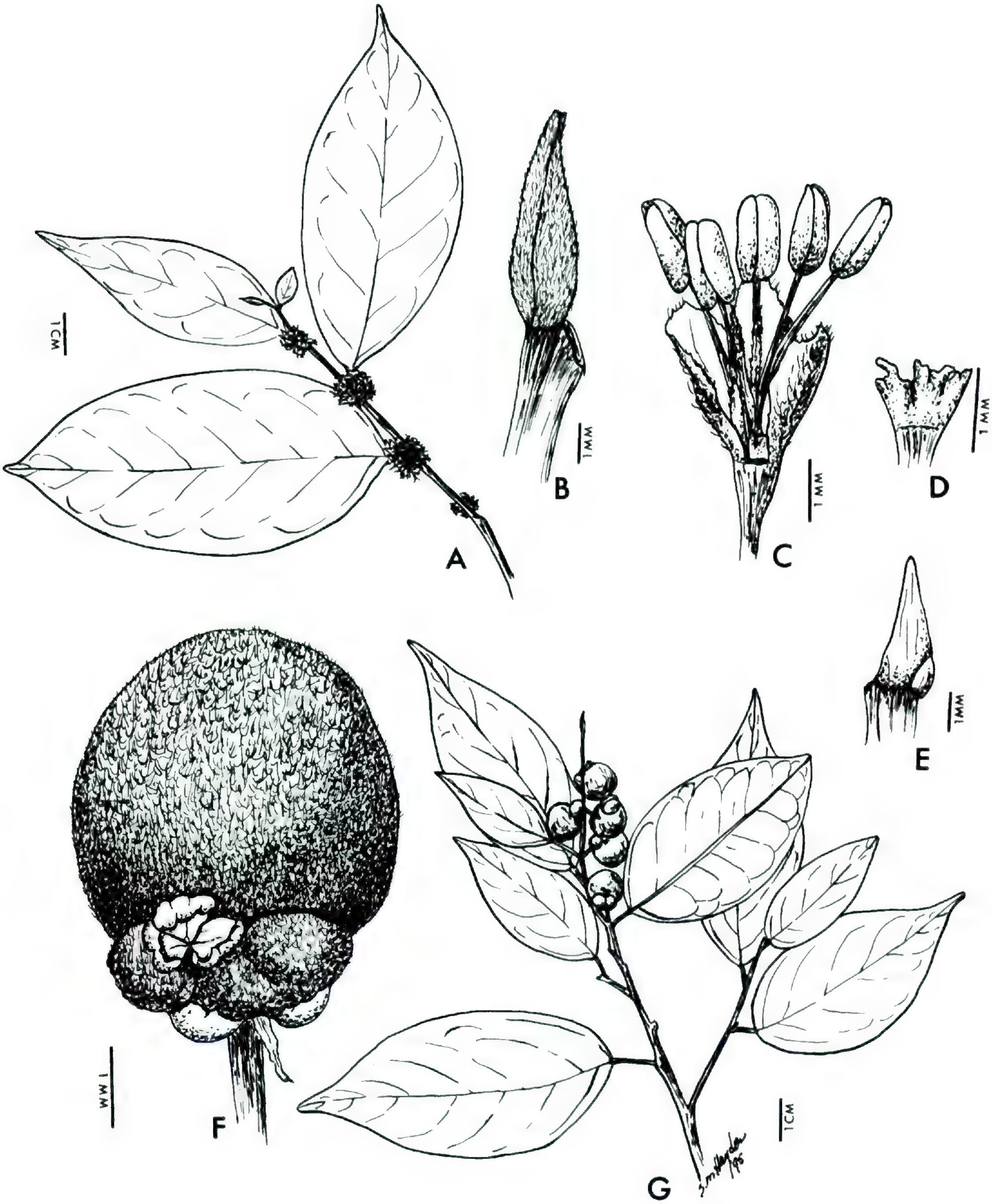


Figure 12. *Discocarpus spruceanus* Müll. Arg. —A. Habit, staminate specimen; *Ducke 904* (F). —B. Terminal bud, staminate specimen; *Mileski 120* (RB). —C. Staminate flower, one sepal removed; *Ducke 904* (F). —D. Disk from staminate flower; *Ducke 904* (F). —E. Terminal bud, pistillate specimen; *Spruce 3527* (BM). —F. Immature fruit; *Davidse 27631* (F). —G. Habit, pistillate specimen; *Spruce 3527* (BM).

ceanus, *Spruce 3527* and *Spruce 3781*, are often curated together leading to potential confusion of the two. Generally, specimens labeled as *Spruce 3781* are staminate and those labeled *Spruce 3527* bear fruits, but the numbers were apparently reversed at G. Further, in many herbaria both Spruce collections are mounted on the same sheet, and fragments from the two are often mixed together in the same packet. An additional confounding factor is that a portion of the duplicates

of *Spruce 3781* has been recognized as the type of a different plant, *Chonocentrum cyathophorum* (Müll. Arg.) Pax & K. Hoffm. (Indeed, one of the two collections of *Spruce 3781* received from OXF was a specimen of *Chonocentrum* misidentified as *Discocarpus spruceanus*; types of *Chonocentrum cyathophorum* have been seen from OXF, G, and NY, confirming that these plants are not *Discocarpus*.) Of the two syntypes, the fruiting collections that constitute *Spruce 3527* are by far more diagnostic than the staminate collection, *Spruce 3781*, and therefore the former serves better as the type. This selection also avoids possible confusion with *Chonocentrum*. Of the several duplicates seen, the specimen from BM is particularly representative.

The sexual dimorphism in terminal buds of *D. spruceanus* is remarkable given that species of *Discocarpus* are otherwise so similar to each other vegetatively. The question whether staminate and pistillate material cited here truly pertain to the same species cannot be dismissed lightly. In southern Venezuela near the Casiquiare–Negro confluence, pistillate plants with the characteristic smooth-surfaced partially aborted fruits occur with staminate plants with hairy buds. No pistillate material of other species has been collected from this area. Further, staminate plants with densely hairy buds do not occur in the Guianas and eastern Brazil, where all pistillate specimens prove to be *D. essequeboensis*, and they are similarly absent from Peru, where pistillate specimens are *D. gentryi*. We therefore interpret staminate specimens with hairy buds and pistillate material with smooth fruits and just a single fertile carpel to be conspecific.

At this writing, we have seen one record of *Discocarpus spruceanus* from Colombia, a flowering staminate specimen, *Little & Little 9604*, collected in 1945.

Excluded Species

Discocarpus duckeanus Jabl., Mem. New York Bot. Gard. 17: 85. 1967. TYPE: *Ducke 33825* (NY) = *Chaetocarpus echinocarpus* (Baill.) Ducke.

Jablonski (1967) based his species on a single collection bearing staminate flowers that, unlike genuine *Discocarpus*, has consistently petal-less flowers with eight (or more?) filaments fused into a central column, and subglobose anthers diverging at various levels. Although present in *Discocarpus*, fusion of filaments is restricted to the base of the flower; the filaments, never more than five, diverge at the same level and terminate in distinctly elongate anthers positioned at approximately the same height. In all respects, Jablonski's species matches *Chaetocarpus echinocarpus* (Acalyphoideae).

Discocarpus mazarunensis Croizat, Bull. Torr. Bot. Club 75: 400. 1948. TYPE: *Fanshawe 2124* (NY) = *Chaetocarpus schomburgkianus* (Kuntze) Pax & K. Hoffm.

When Croizat (1948) named his new species, based strictly on staminate material, he noted that its vegetative features were discordant with those of *Discocarpus*. Jablonski (1967) accepted *D. mazarunensis* without comment. In recent years, Michael Huft annotated several specimens of *Discocarpus mazarunensis* as *Chaetocarpus schomburgkianus*, and Gillespie (1993), following his lead, excluded this species from *Discocarpus*. As in the case described above, the flowers in the type of *D. mazarunensis* have filaments fused into a prominent staminal column with anthers diverging at different levels. Exclusion from *Discocarpus* is thus justified.

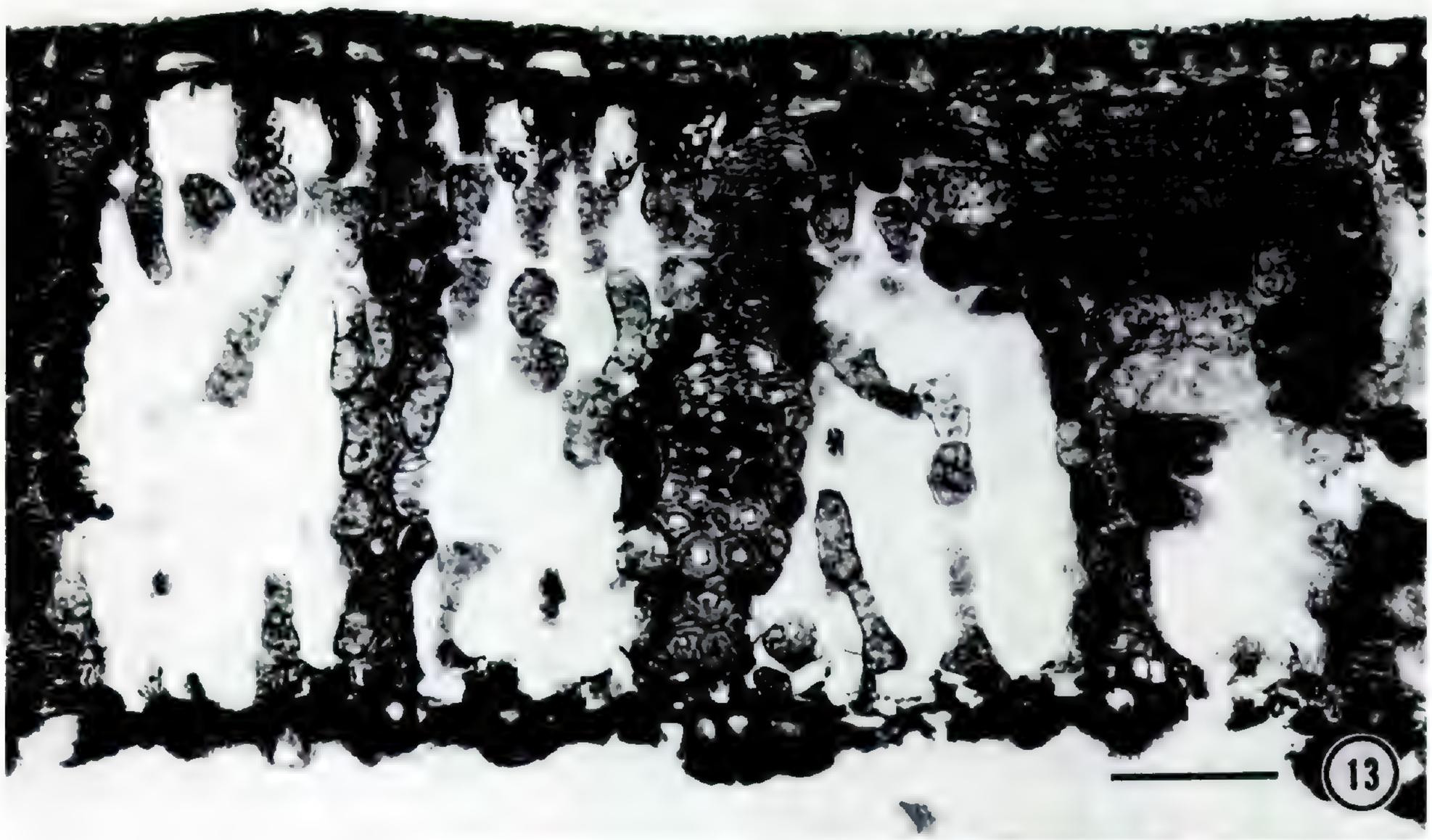
Discocarpus mexicanus Liebm., Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 5: 309. 1851 = *Laportea mexicana* (Liebm.) Wedd. (Urticaceae) (as per Pax & Hoffmann, 1922).

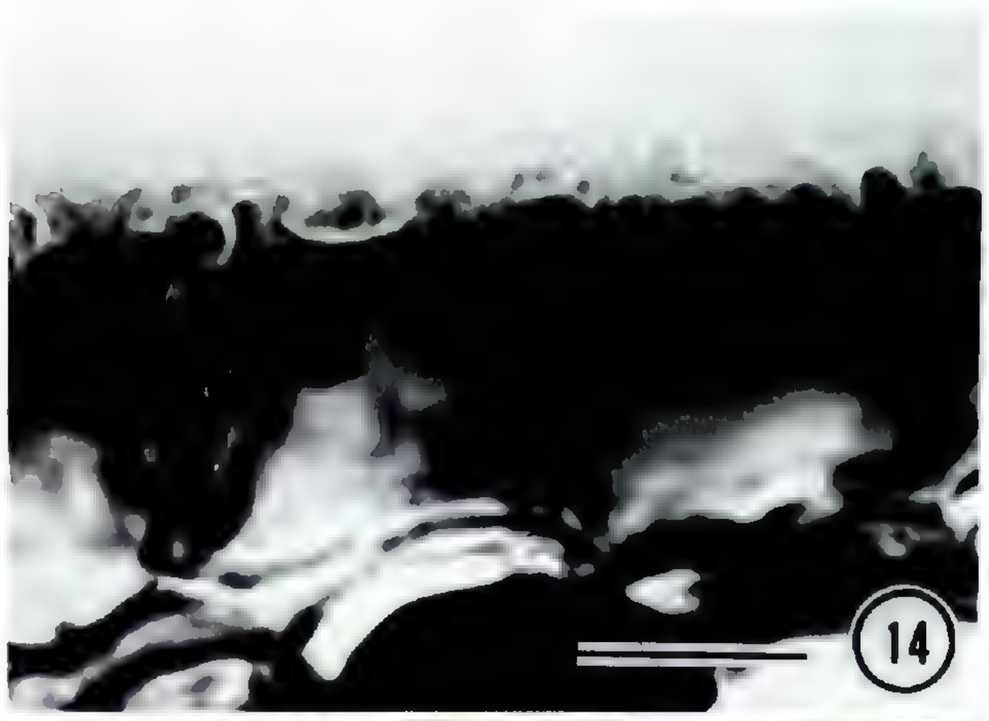
Discocarpus nicaraguensis Liebm., Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 5: 309. 1851 = *Laportea nicaraguensis* (Liebm.) Wedd. (Urticaceae) (as per Pax & Hoffmann, 1922).

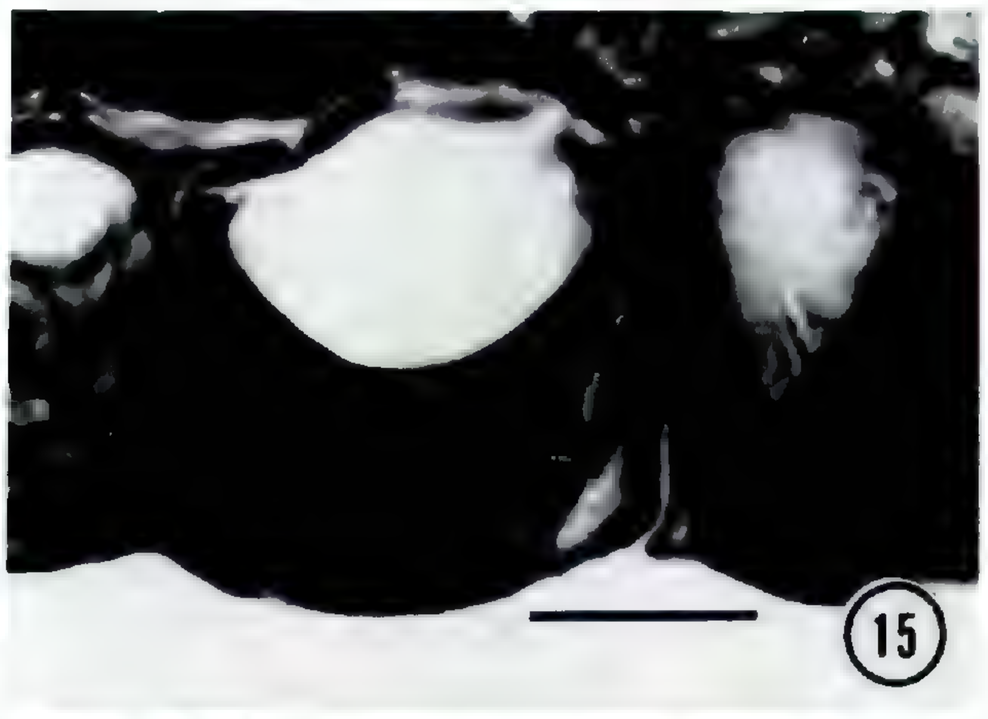
Foliar Anatomy

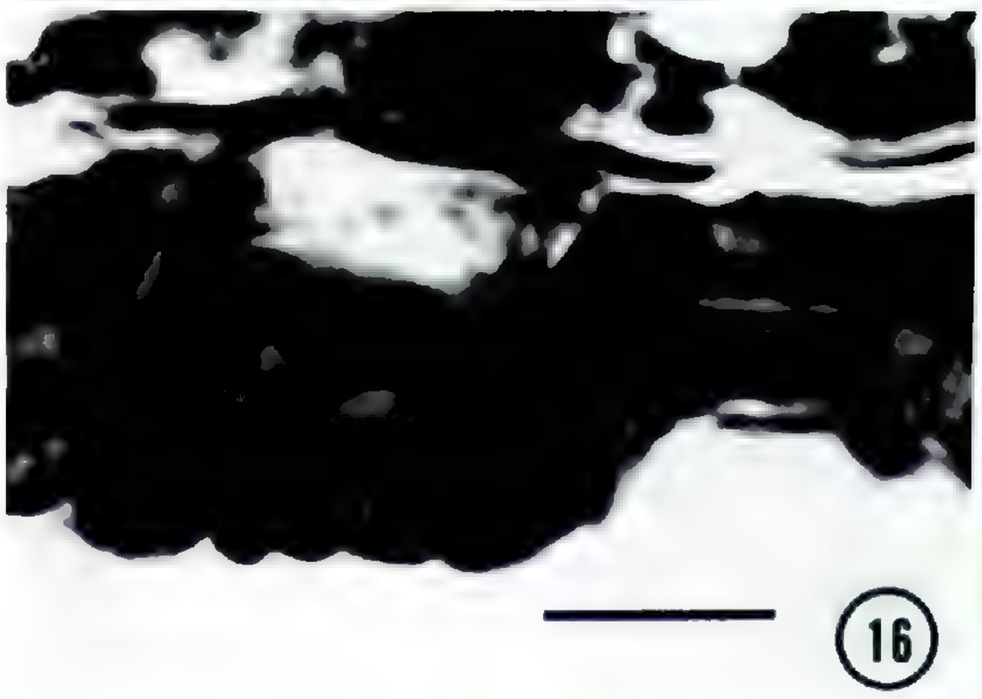
Leaf anatomy was found to vary little from species to species, hence the following descriptions pertain to all three species. Dimensions cited are average values based on 10 measurements of each feature per specimen.

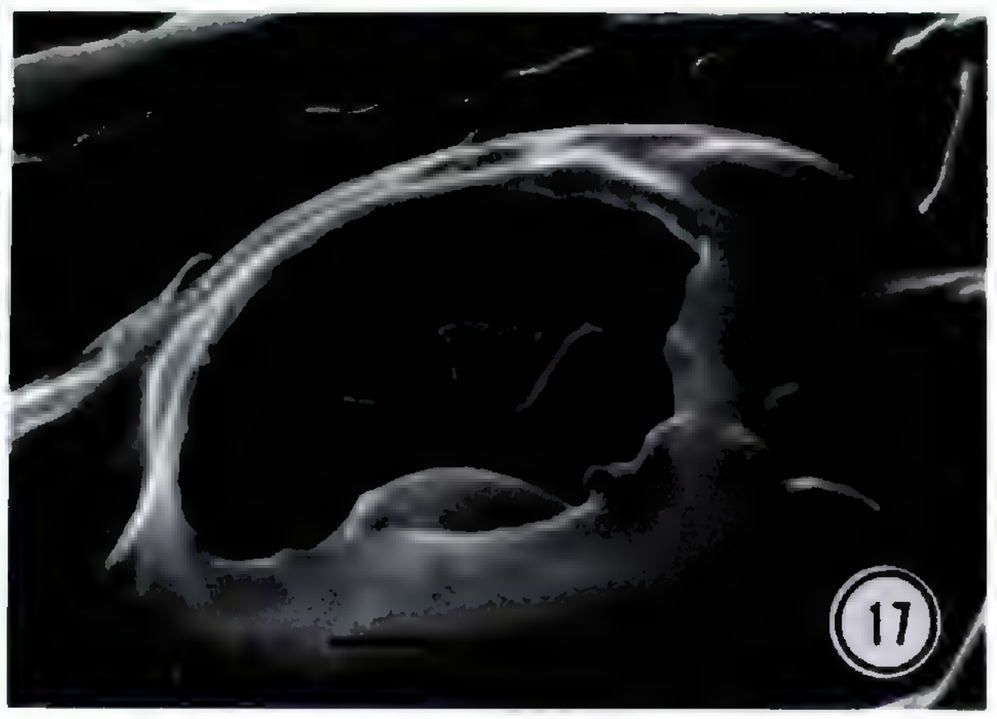
Epidermis (both adaxial and abaxial) uniseriate; cells irregular, partially sclerified; outer periclinal walls sclerified; anticlinal walls wavy, sclerified unevenly, thicker toward the surface, thinner toward the mesophyll (occasional cells of adaxial epidermis sclerified on inner periclinal wall, thinner along anticlinal wall outward); outer periclinal walls bearing subcuticular micropapillae (best seen in *Discocarpus spruceanus*, Figs. 14, 15, 16). Adaxial epidermal cells 15 μm thick, uniformly bearing tannin deposits; cuticle 1–2 μm thick. Abaxial epidermal cells 11 μm thick, occasionally bearing tannin deposits; cuticle <1 μm thick. Stomata restricted to the abaxial epidermis, densely crowded,











Figures 13–17. Foliar anatomy of *Discocarpus*. 13–16, *Discocarpus spruceanus* Müll. Arg., *Wurdack & Adderly 43349* (NY). —13. Leaf cross section; bar = 50 μm. —14. Sclerified adaxial epidermis with micropapillae; bar = 10 μm. —15. Sclerified abaxial epidermis below vein; bar = 10 μm. —16. Sclerified abaxial epidermis with micropapillae; bar = 10 μm. —17. *Discocarpus gentryi* S. M. Hayden, *Rimachi Y. 3281* (NY). SEM of stomate with crenulate anticlinal wall of guard cell; bar = 5 μm.

oriented randomly, widely elliptic, 18 μm long, 15 μm wide; anticlinal walls forming stomatal pore minutely crenulate (Fig. 17); subsidiary cells brachyparacytic.

Mesophyll stratified, tannin deposits scattered throughout; palisade cells well developed, sometimes lightly sclerified near the adaxial epidermis; spongy layer weakly developed, vertically oriented, intercellular spaces large, druses present (Fig. 13).

Large veins composed of concentric arcs of xylem and phloem bounded above and below with groups of fibers; small veins vertically percurrent

by fibrous bundle sheath extensions sheathed with a single layer of parenchyma (Figs. 13, 20); cells of the parenchyma sheath frequently bearing prismatic crystals (Fig. 19). Areoles well developed, quadrangular, oriented (Fig. 18).

The combined presence of many sclerified cells, thick-walled fibers, prismatic crystals, and druses render leaves of *Discocarpus* physically tough and durable. While the anatomical preparations described above conform generally with previously published information, neither Gaucher (1902) nor Levin (1986) mentioned the existence of sclerified cells in the adaxial layer.

Discussion of Relationships

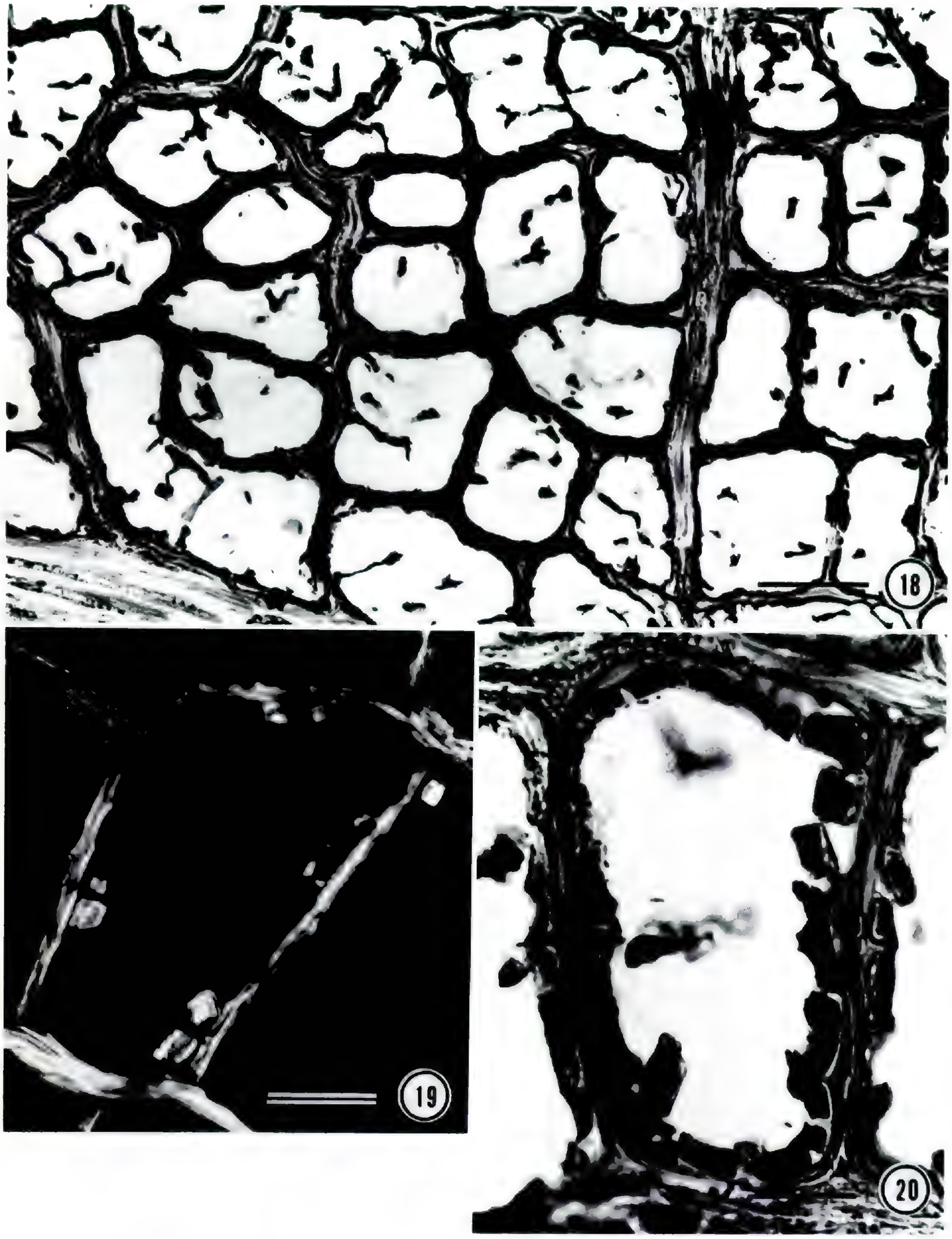
In this century, *Discocarpus* has been assigned to subtribe Discocarpinae of tribe Phyllantheae (Pax & Hoffmann, 1922, 1931). Köhler (1965) suggested placement in Bridelieae. Hutchinson (1969) did not include the genus in any of his proposed tribes. Most recently, Webster (1975, 1994b) has placed *Discocarpus* in tribe Wielandieae, an assemblage of primitive mostly petal-bearing phyllanthoid genera. At the generic level, *Discocarpus* has been most closely associated with *Lachnostylis* and *Chonocentrum*; in Webster's (1994b) classification, all three genera are placed in Wielandieae and key out adjacent to each other. In fact, the South African genus *Lachnostylis* was combined with *Discocarpus* by Pax and Hoffmann (1922).

The small trees and shrubs of *Lachnostylis* grow in much drier habitats than neotropical *Discocarpus* and, thus, the plants appear different superficially. However, when one looks beyond the much smaller leaves and highly branched stems, details such as flowers, areolation, and shape of terminal buds support Pax and Hoffmann's (1922) earlier view. To distinguish *Lachnostylis* from *Discocarpus*, Webster (1994b) cited thin styles, pubescent staminate disks, and stamens adnate to the pistillode in the former. However, cursory examination reveals thick styles in *Lachnostylis* similar to those of *Discocarpus* in at least some specimens, and pubescence of the disk may be little more than a reflection of the overall hairier aspect of *Lachnostylis*. Most importantly, as documented herein for *Discocarpus* (Figs. 1, 2), staminate flowers of both genera have connate filaments adnate to the base of the pistillode. Hence, the relationship between *Lachnostylis* and *Discocarpus* seems extremely close.

In contrast, relationship with *Chonocentrum* is much less likely. *Chonocentrum* first became associated with *Discocarpus* by accident. As discussed above, type collections of *Discocarpus spruceanus* and *Chonocentrum* bear the same collection number, *Spruce 3781*, as a result of mixing these clearly distinct plants. *Chonocentrum* is still known only from the type collection, so comparative data are scarce, and Webster (1994b) considered any possible relationships with this genus to be uncertain. Cursory examination of several isotypes of the only species in the genus, *C. cyathophorum*, shows this plant to be clearly distinct from *Discocarpus*. The cuplike fused calyx, complete absence of petals, and large funnelform pistillode contrast sharply with *Discocarpus* and have no counterpart in Wielandieae. Although Webster (1994b) stated that the pollen of *Chonocentrum* is unknown, Punt (1962) placed the genus in his "*Antidesma* type," noting that the grains are "quite different" from those of *Discocarpus*. Given its ament-like staminate inflorescence, fused calyx, and absence of petals, *Chonocentrum* keys readily to Webster's (1994b) tribe Antidesmeae, a context within which further comparative studies should prove fruitful. The cuplike calyx of staminate flowers of *Hyeronima* Allemão (Franco R., 1990) and the funnel-like pistillode of *Cyathogyne* Müll. Arg. (Pax & Hoffmann, 1931), both members of subtribe Antidesmineae, appear directly comparable to structures found in *Chonocentrum*.

Two previously unappreciated characters may serve as synapomorphies that argue for a novel taxonomic placement of *Discocarpus* (including *Lachnostylis?*) near *Amanoa* (tribe Amanoeae). First, neotropical *Discocarpus* and *Amanoa* share the unique feature of sclereids in the epidermis, which is otherwise unknown in the Euphorbiaceae (Gaucher, 1902; Levin, 1986) and extremely rare among dicots. Presence of foliar epidermal sclereids is likely synapomorphous for these genera. Second, staminate flowers of *Discocarpus*, *Lachnostylis*, and at least two species of *Amanoa*, *A. nanayensis* W. J. Hayden and *A. steyermarkii* Jabl. (Hayden, 1990), share an androgynophore-like structure (sometimes described as filaments connate to the pistillode); this feature, too, is likely synapomorphous for these genera (Webster, 1994a). In addition, while several genera of Wielandieae possess scalariform perforation plates in the wood, *Amanoa* and *Discocarpus* (as well as *Lachnostylis*) share the derived state of simple perforation plates (Mennega, 1987; Hayden et al., 1993). Based on wood features, Mennega (1987) argued for the exclusion of *Discocarpus* from Wielandieae.

Superficially, inflorescences of *Discocarpus* and *Amanoa* appear distinctly different; however, their basic architecture may prove to be homologous. As described and illustrated here, flowers of *Discocar-*



Figures 18–20. Foliar anatomy of *Discocarpus*. —18. *Discocarpus gentryi* S. M. Hayden, *Vásquez & Jaramillo 5487* (NY). Areoles between veins in paradermal section; bar = 100 μm. 19, 20, *Discocarpus essequeboensis* Klotzsch, *Smith 2692* (F). —19. Prismatic crystals associated with parenchyma cells lining the areoles; polarized light micrograph; bar = 40 μm. —20. Parenchyma cells lining areoles; bar = 40 μm.

pus occur in axillary clusters. Substructure within these clusters is difficult to discern in the dried, pressed specimens available for study; however, their placement appears to be consistent with the sessile cyme diagrammed for *Amanoa* by Pax and Hoffmann (1922). Thus, while the cymes of *Discocarpus* occur in the axils of foliage leaves and those of neotropical *Amanoa* are placed in the axils of reduced bracteal leaves, the differences between these genera are neither great nor absolute in this regard. It should be noted that cymes of some African *Amanoa* are axillary to foliage leaves. While *Amanoa* is largely monoecious, *Amanoa anomala* Little (Little, 1969) is dioecious, as is *Discocarpus*. It is also noteworthy that Punt (1962) and Köhler (1965) distinguished the pollen of *Discocarpus* from

that of other Wielandieae. Although pollen differences with *Amanoa* exist, Punt (1962) included *Discocarpus* as a distinct type under his "*Amanoa* configuration." Thus, inflorescence architecture, flower structure, foliar anatomy, wood, and pollen, all support classification of *Discocarpus* in tribe Amanoeae as superior to its present placement in Wielandieae.

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A REVISION OF THE FERN GENUS *PHANEROPHLEBIA* (DRYOPTERIDACEAE)[1]

George Yatskievych[2]

Abstract

The primarily neotropical fern genus *Phanerophlebia* is revised taxonomically to include eight species, with a key and descriptions provided. Classification of the genus within the Dryopteridaceae is reviewed, as are the morphology, stelar anatomy, and cytology of the species. The justification for reduction of *Phanerophlebia remotispora* to a variety of *P. nobilis* is discussed. The recently named diploid species, *P. gastonyi*, is contrasted with its tetraploid derivative, *P. juglandifolia*, and hybridization and polyploidy within the genus are summarized.

Phanerophlebia C. Presl is an enigmatic genus comprising eight species of terrestrial ferns of the New World tropics and adjacent subtropical regions. Most pteridologists know little about the group because of the rarity with which the species are encountered in nature. The genus was revised taxonomically by Underwood (1899) and Maxon (1912). Both of these early studies were based on relatively few herbarium specimens and did not adequately circumscribe variation in critical morphological characters, resulting in many subsequent misdeterminations.

The need for a new taxonomic study of this genus was further supported by disagreements and questions raised by the few researchers who have examined the species in recent years. Smith (1981), Mickel and Beitel (1988), and Stolze (1981), in their detailed floristic treatments of pteridophytes of Chiapas and Oaxaca, Mexico, and Guatemala, respectively, each pointed out taxonomic problems in the group and emphasized different characters in delineating taxa. Tryon and Tryon (1982), in their review of American ferns, pointed out the confusing pattern of morphological variation in the genus and suggested that some of the traditionally accepted species might be combined, following much-needed, critical, future studies.

Aside from questions of species-level taxonomy, *Phanerophlebia* has also provided problems in generic classification. The distinctness of the group from Asiatic *Cyrtomium* and nearly cosmopolitan *Polystichum* has remained controversial and is symptomatic of the general difficulties of generic circumscription present in the family Dryopteridaceae (and in several other pteridophyte families as well).

The present paper incorporates data from several concurrent studies (Stein et al., 1989; Yatskievych, 1989, 1990, 1992, 1993; Yatskievych & Gastony, 1987; Yatskievych et al., 1988) on aspects of evolution and systematics of *Phanerophlebia* and the results from field, herbarium, and greenhouse studies on the group, in an attempt to refine our understanding of the genus. An evolutionary species concept is employed, which circumscribes a set of morphologically defined taxa that are also genetically separated. Genetic separation, based on various estimates of genetic similarity, rather than crossing barriers, has been used, because attempts at artificial hybridization between taxa failed uniformly (unpublished data). The varietal designation is used in this paper to denote putatively interfertile morphotypes within a species, which lack sharp biogeographic discontinuities, and which are sep-

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arated by only a single, relatively trivial, morphological character (whose genetic basis remains unknown).

Methods and Materials

Herbarium specimens, including types, were studied from the following collections: A, ARIZ, ASC, BH, CAS, CM, CR, CU, DS, ENCB, F, GH, HAL, IND, K, LL, MEXU, MICH, MO, NY, P, POM, RSA, TEX, UAMIZ, UC, US, XAL (abbreviations follow those used in Holmgren et al., 1990). Approximately 1400 specimens representing about 670 different collections of *Phanerophlebia* were examined. Additionally, about 260 collections of *Cyrtomium* and *Polystichum* were examined for comparative purposes.

Information from herbarium specimens was supplemented with observations of populations in nature. A total of 25 populations of *Phanerophlebia* was located during fieldwork in the southwestern United States, Mexico, and Costa Rica. In addition to field observations and carefully pressed specimens, representative plants from each population were transplanted into common culture in the Department of Biology greenhouses at Indiana University for further observation of phenotypic variation.

For detailed observations of scale morphology, small strips of clear tape (Scotch) were used to remove samples from leaves and rhizomes with the aid of forceps and mounted on microscope slides in Hoyer's medium. Stelar observations were based on direct observation of freehand sections from living rhizomes. Details of venation patterns and epidermal morphology were observed from pinnae or pinna pieces cleared using the bleaching procedures summarized by Dilcher (1974). Following dehydration and staining with safranin O, samples for observation of leaf venation were dried flat in a small press similar to that described by Wagner (1976), and epidermal samples were mounted on microscope slides in Permount, prior to viewing.

Chromosome counts were made on representatives of each population. Young pinnae with developing sporangia were fixed in Farmer's solution (3:1 absolute ethanol:glacial acetic acid) for meiotic counts. Sporangia were spread using the standard acetocarmine squash technique (Manton, 1950), as modified by Haufler et al. (1985). Cells were examined with a compound microscope and chromosomes were drawn using a camera lucida. New counts or those differing from the literature were also photographed, using Kodak Technical Pan film.

For spore counts, single, unopened sporangia were carefully removed from field-collected (rather than greenhouse-grown), dried pinnae with a dissecting probe and opened in a drop of lactic acid under the dissecting microscope. Ten counts from different sori were compiled for representative plants from each population. Spore sizes were also measured from material in lactic acid, using a compound microscope equipped with an ocular micrometer. Thirty measurements of the longest dimensions of spores from at least five sporangia were made, from which the mean and standard deviation were calculated for each sample. Spore morphology was observed under the compound microscope from material in lactic acid and from dried material, as well as by scanning electron microscopy (SEM). The latter observations were carried out using a Cambridge Stereoscan 250-MK2 machine. Dry spores were mounted on aluminum SEM stubs using double-sided tape without pretreatment and sputter-coated with gold/palladium using a Polaron E5100 unit prior to viewing.

Morphology and Anatomy

Rhizomes and Leaves

Rhizomes of *Phanerophlebia* species are dictyostelic and anatomically similar to those of *Cyrtomium* species studied by Chandra and Nayar (1982) and Gibson et al. (1984). They range from 3 mm in diameter in small plants of *P. pumila* to ca. 20 mm in *P. macrosora*, but are 8–15 mm in adult plants of most species. Rhizomes may be characterized as generally short-repent (erect or ascending in *P. macrosora* and *P. pumila*), unbranched (tending to branch at maturity in *P. auriculata* and *P. umbonata*), and deep-seated in the substrate (except in *P. gastonyi*, *P. pumila*, and sometimes in *P. juglandifolia*). In all species, the rhizomes are densely covered with scales near the apices and with persistent petiolar bases and adventitious roots on older portions. The dense mat of petioles and roots makes the rhizomes appear larger than they actually are. Rhizome scales are discussed below, under indument.

Leaves (fronds) develop equally from all sides of the rhizomes and are clustered near the rhizome apices. Mature leaves range in length from 4 cm in *P. pumila* to 270 cm in *P. macrosora*. They persist for two or more years and eventually die back to the petiolar bases, which are persistent. There is no well-defined zone of abscission along the petioles. The petiolar bases persist for several years, turning hard and "woody" in *P. macrosora*, but remaining green and semisucculent, with green in-

ternal tissues, in other species. Although an iodine test was not performed, these persistent petiolar bases presumably function as trophopods (Wagner & Johnson, 1983).

Petiole vascularization is simpler than in many other members of the Dryopteridaceae, and the 4–8 vascular bundles (mean = 6) are arranged in an uneven ring. The petioles are curved abruptly at their bases, so as to orient the leaves vertically, except in *P. macrosora*. In this species the petiolar bases are usually oriented horizontally for a distance of 5–10 cm, before curving upward, the leaf bases thus appearing geniculate. Petioles may be shorter than or somewhat longer than the laminae, and are scaly (see below) in all species.

Laminae are monomorphic and 1-pinnate (sometimes simple in *P. gastonyi* and *P. pumila*), with alternate pinnae (leaflets). Rachises are adaxially sulcate, with the groove more or less confluent with the costal groove of each pinna, although, in practice, this character is usually difficult to assess. The laminae have discrete terminal pinnae, but are not typically imparipinnate in that some leaves of all species have an even total number of pinnae. Such leaves are usually mixed on the same plant with those having odd numbers of pinnae, and there is no morphological evidence for the existence of "pseudoterminal" pinnae; i.e., no nodes or articulations are present at the tip of a rachis to suggest suppression of the laminar apex and its replacement by an adjacent, lateral pinna.

Pinnae of all species are chartaceous to subcoriaceous and have shallow, adaxial, costal grooves. They range in shape from ovate to linear-lanceolate and commonly have attenuate apices and asymmetrical bases. Pinna bases are normally more developed acroscopically (Fig. 1), and acroscopic, basal auricles occur commonly in *Phanerophlebia auriculata*, sporadically in *P. pumila*, and rarely in *P. nobilis* (var. *nobilis*). Pinna margins are spinulose-serrulate, the teeth connected by a narrow, white, marginal band of hard tissue, but the density and distribution of the teeth vary. In *P. gastonyi*, the serrulations are confined to the distal half of each pinna, and in *P. juglandifolia* the density of serrulations in proximal portions of the pinnae can vary greatly on individual leaves. In *P. macrosora*, serrulations tend to be somewhat more widely spaced than in other species and the teeth are often somewhat stouter.

Rare individuals of most species (particularly *Phanerophlebia auriculata* and *P. pumila*) have some leaves with the pinnae deeply incised to lacerate, particularly on the acroscopic side (Fig. 1b). The same phenomenon was described by Wagner (1979) for *Polystichum munitum*, and a similar phenomenon in *Polystichum acrostichoides* (f. *incisum* (A. Gray) Gilbert) was attributed by Wagner et al. (1970) to environmental and temporal factors. In *Phanerophlebia*, it is of interest to note that in such pinnae the lobes each contain one vein that has branched from the costa and that the multiseriate (with respect to the costa) sori are arranged in a single series on either side of this midvein in each lobe. Such anomalous pinnae provide indirect evidence that the 1-pinnate leaf dissection in *Phanerophlebia* is derived from a more highly dissected leaf type.

Venation in *Phanerophlebia* species is anadro-

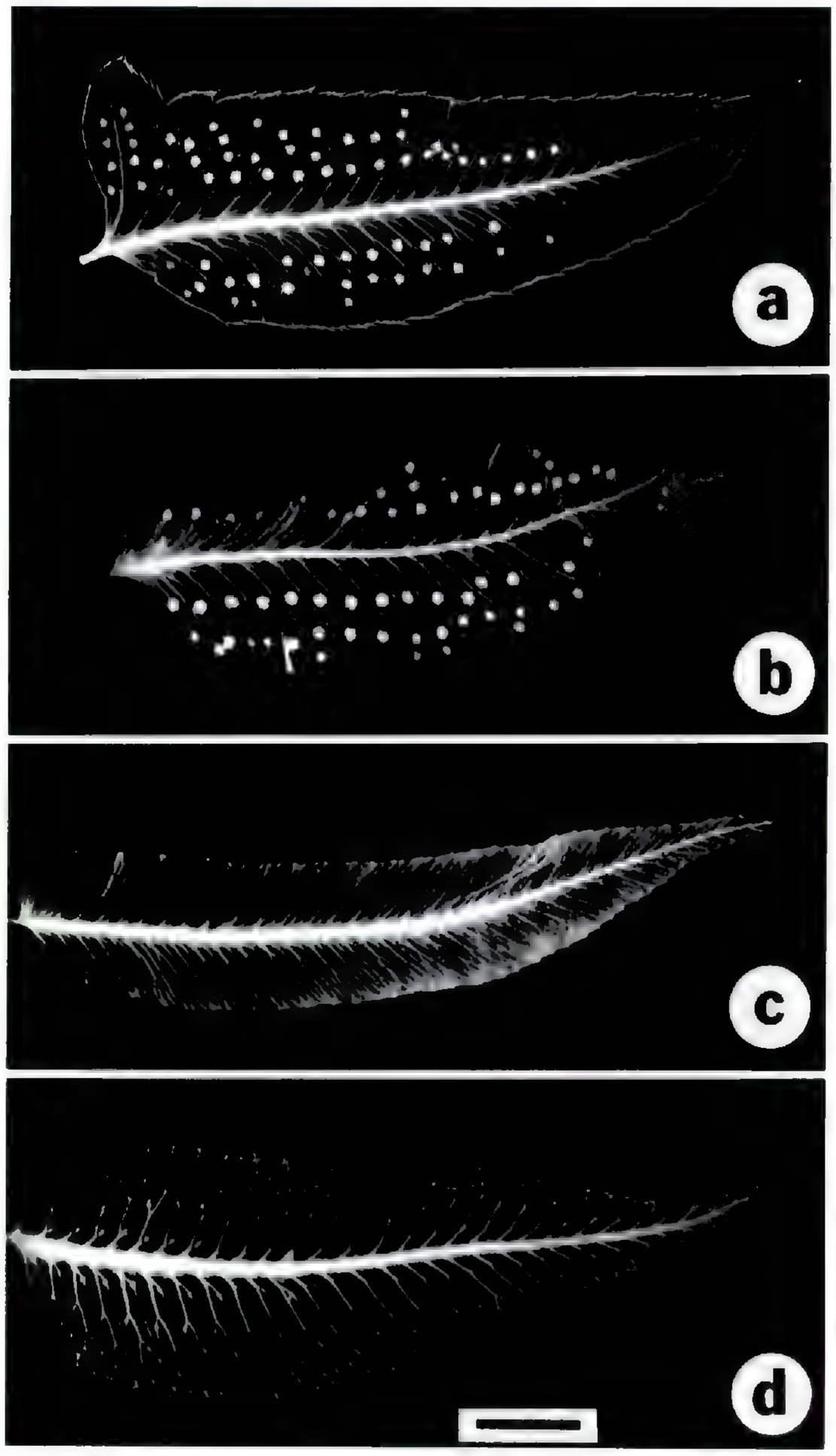


Figure 1. Cleared pinnae of *Phanerophlebia* species. —a. *P. auriculata* (*Yatskievych et al. 83–10*), showing simple, dichotomous venation and presence of acroscopic, basal auricle. —b. *P. auriculata* (*Yatskievych et al. 84–68*), showing irregular acroscopic lobing. —c. *P. umbonata* (*Yatskievych & McCrary 85–05*), showing simple (non-anastomosing), dichotomous venation. —d. *P. gastonyi* (*Yatskievych et al. 85–182*), showing anastomosing venation. Scale bar = 1 cm.

mous (this often difficult to observe) and consists of numerous, arcuate, secondary veins branching sequentially from the costa of each pinna (Fig. 1). These secondaries branch 1–4 times before terminating near the pinna margin. There is no vein running parallel to the margins, but there is a thickened, narrow band of hard, white tissue along the edge, at which the veins terminate. Thus, the veins do not extend into the marginal serrulations of the pinnae. The basal 1–2 vein branches do not extend to the margins, instead terminating between the costa and margin. Vein endings are tapered (except those terminating in sori), lacking bulbous thickenings.

The venation pattern of *Phanerophlebia* is of two kinds. The most common type, which characterizes all taxa except *P. gastonyi*, *P. juglandifolia*, and *P. nobilis* var. *remotispora*, consists of simple, dichotomously branched secondaries essentially lacking anastomoses (Fig. 1a–c). All of the free-veined taxa can produce rare, marginal anastomoses, and in *P. haitiensis* these can be fairly common (>2 per pinna, but very irregularly distributed). The ultimate vein-branches in the free-veined taxa range from arcuate to nearly straight, but are usually more or less parallel to one another.

In *Phanerophlebia gastonyi*, *P. juglandifolia*, and *P. nobilis* var. *remotispora*, the branching secondary veins form a regular pattern of 1–3 series of simple, submarginal anastomoses (Fig. 1d). The pattern of reticulation is that of elongate areolae with acute apices and bases. There are no free, tertiary veins included in the reticulations (as in *Cyrtomium*), but in most cases the basal branches of the secondaries end below the anastomoses of adjacent, more marginal branches, thus appearing enclosed. Although there are no clear morphological distinctions between the patterns of reticulation found in the closely related *P. gastonyi* and *P. juglandifolia* on the one hand and those of *P. nobilis* var. *remotispora* on the other, evidence from restriction site polymorphisms in the chloroplast genomes (Yatskievych et al., 1988) and the fact that only one of the two varieties of *P. nobilis* exhibits reticulate venation suggest that this pattern has arisen independently twice in the genus.

Sori of *Phanerophlebia* species are either terminal or lateral on the secondary veins and are situated in 2–4 series (sometimes only 1-seriate in *P. pumila*) between the costa and margin. In *P. umbonata*, the sori are sometimes clustered submarginally, but otherwise they occur in a broad band between the costa and each margin. In *P. gastonyi* and *P. juglandifolia* (occasionally also in other species) the innermost series of sori may be situated less than 2 mm from the costa, but the innermost sori are otherwise normally more than 4 mm from the costa. This character has been used by some authors to differentiate *P. juglandifolia* from *P. nobilis* var. *remotispora*, but is too variable for consistent application.

The sori are more or less circular and in all but two taxa are covered by an indusium. Presl (1836) first noted the absence of an indusium in *Phanerophlebia juglandifolia* (which he used as evidence to align this species with *Polypodium* under the generic name *Amblia*), but nearly all subsequent workers ignored or dismissed this character until it was reexamined by Smith (1981). *Phanerophlebia gastonyi*, which has been confused with *P. juglandifolia* in the past, is the other species lacking indusia. Part of the problem with regard to this character is that in all of the indusiate species except *P. umbonata* the indusia are fugacious, shriveling and mostly falling off by the time the sorus is mature. Thorough examination of sori in these taxa will always result in the discovery of at least a few remaining, shriveled indusia, however.

In those species possessing indusia, these ephemeral structures are light tan, peltate, roughly circular in outline, erose-margined, and 0.6–1.1 mm in diameter. They are membranous to papery, concolorous, and flat to slightly concave centrally, except in *Phanerophlebia umbonata*, which has firmer, subcoriaceous, persistent indusia with a raised, darkened umbo in the center. Indusia of *P. pumila* are unusual in that the attachment point of the receptacle is sometimes acentric, and the indusia are often more ovate than circular in outline. It is also of interest that although diploid *P. gastonyi* and its tetraploid derivative, *P. juglandifolia*, lack indusia, the rare, sterile, triploid hybrid between the latter taxon and the indusiate *P. macrosora* has rudimentary, irregular indusia less than 0.2 mm in diameter.

SPORES

Spores of selected *Phanerophlebia* species were examined cursorily (usually in conjunction with those of *Cyrtomium*) by several earlier authors, but the first detailed study of spore morphology in the genus appeared as part of the generic treatment for *Cyrtomium* (including *Phanerophlebia*) in Tryon and Tryon's (1982) broad survey of fern genera. The subsequent discussion in Tryon and Lugardon's (1991) survey of fern spores expanded slightly on this initial treatment. The present account attempts to expand upon this excellent foundation.

Sporangia contain 64 spores in all fertile taxa

and are monolete and dark brown at maturity. Spores fall into three size classes. Those of the diploid *Phanerophlebia gastonyi* are 30–42 μm in longest dimension, whereas those of other fertile diploid and tetraploid taxa in the genus are 41–60 μm. Spores of *P. haitiensis*, although seemingly well formed, show great size variation, even within individual sporangia, and measure 36–52 μm. Spore size is thus of little use in identifying polyploids, except as a means of distinguishing *P. gastonyi* from its closest relatives.

The exospore in all species is smooth (Fig. 2) and is covered by a two-layered perispore. The thin, inner perispore has a slightly undulate surface, often also with widely scattered papillae. These papillae may represent the rudiments of columellae that once connected the inner and outer perisporal layers, but actual columellae apparently no longer exist. The outer layer of perispore is much thicker than the inner layer and consists of inflated, irregularly undulate folds. The density and degree of inflation of these folds varies developmentally and within each species. They are thus of little use in distinguishing among them, although the mature spores of *P. macrosora* generally have fewer folds than those of other taxa. The surface of the outer perisporal layer also varies from nearly smooth to rugulose and contains no observable microperforations.

All fertile specimens of *Phanerophlebia* species possess at least some sporangia that, at maturity, contain malformed, apparently abortive spores of variable size with the outer perisporal layer relatively smooth and the folds winglike and uninflated (Fig. 2d). These resemble immature spores in their incomplete perisporal deposition and although not obviously collapsed or shrunken within, they will not germinate on agar or soil. Sporangia containing such spores are especially frequent in the relatively few herbarium specimens available of *P. haitiensis*. Whether this phenomenon has a genetic basis is not presently known, but plants placed under environmental stress (such as excess sunlight or high temperature) in the greenhouse produce such abortive spores with greater frequency than when grown under more optimal conditions.

INDUMENT

Leaves of *Phanerophlebia* species do not possess true hairs in the sense that this term is usually applied to such epidermal outgrowths in most ferns. Instead, the uniseriate, multicellular trichomes present in all species are in reality reduced scales, and intergrade completely with the larger, pluriseriate structures usually associated with this term (Fig. 3). Such reduced scales are common in the Dryopteridaceae and have been noted by several students of the family. Daigobo (1972) believed that variations in the pattern of cellular orientation and shape made such trichomes the most stable and important characters for infrageneric classification of the 47 species of *Polystichum* in Japan, Ryukyu, and Taiwan, and applied the name "microscale" to them. Viane (1986), who held trichome morphology to be important in classification of *Dryopteris* species, adopted the name "paleaster" for such hair/scale intermediates. Moran (1986, 1987), working with the related genera *Olfersia* and *Polybotrya*, coined the term "proscale" for them. Smith (1986), in his monograph of *Cyclodium*, differentiated reduced scales from acicular hairs and septate glands also found in that genus but declined to invent a name for these structures. Barrington (1989), in his studies of neotropical *Polystichum*, adopted the term "microscale" and noted that most species of neotropical *Polystichum* shared Daigobo's (1972) *Metapolystichum* type of scale development.

The pattern of scale development in all species of *Phanerophlebia* is identical and is similar to that seen in the *Metapolystichum* type of Daigobo (1972). The reduced scales found to some degree on the abaxial laminar and distal costular surfaces are tan to brownish and appressed. The smallest are uniseriate and approximately 3 cells long, with somewhat flattened cells and thickened endwalls. In contrast to the situation described by Daigobo (1972) for *Metapolystichum*, however, the terminal cells of these smallest scales are obtuse, rather than acutely attenuate (Fig. 3). Larger scales with two or more cellular series display the morphology more typical of *Metapolystichum* scales. In these larger, reduced scales the basal 1–2 series of cells are smaller than the other cells and are nearly square to rhomboidal in outline. Above this base, the body of the scale is broadened and the individual cells are elongate longitudinally. Processes homologous to the lateral cilia of fully developed costal and petiolar scales are first evident near the base of the reduced scales, which are otherwise entire along their lateral margins.

Along the costae, the reduced scales grade abruptly into the longer and broader structures usually associated with the term scale. Reduced scales are best observed on immature leaves and are apparently shed during development or at least easily abraded from mature laminae. The pinnae of some populations of *P. auriculata* and *P. pumila* possess the densest covering of reduced scales, but this retention of vestiture may be due primarily to the

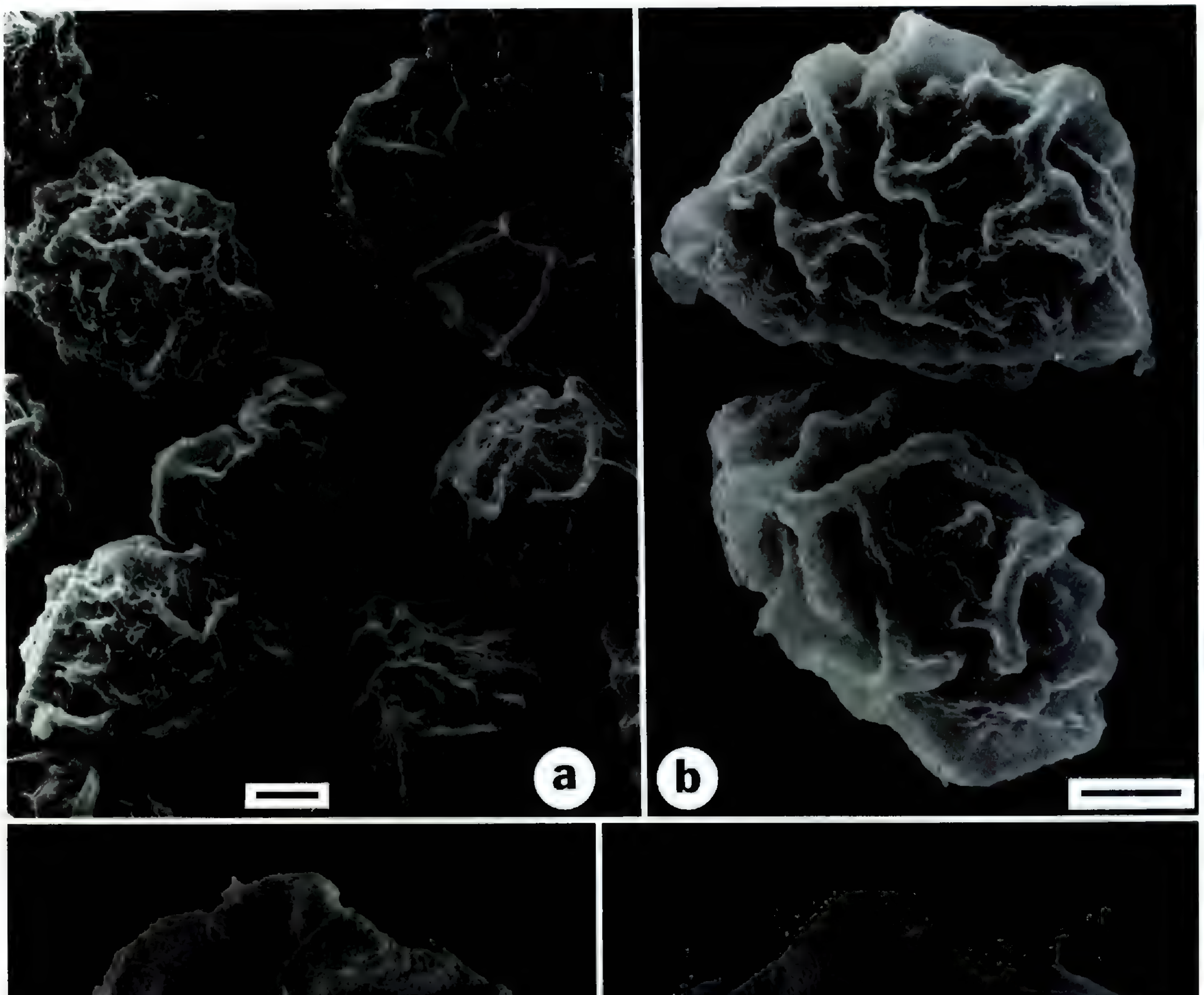


Figure 2. Spores of *Phanerophlebia* species. —a. *P. umbonata* (*Yatskievych & Wollenweber 83–87*), a mixture of mature and immature spores. —b. *P. auriculata* (*Yatskievych et al. 83–10*). —c. *P. gastonyi* (*Yatskievych et al. 85–182*). —d. *P. macrosora* (*Yatskievych & McCrary 86–30*), with incomplete perispore formation characteristic of nonfunctional spores present in some sporangia of all species. Scale bars = 10 μm.

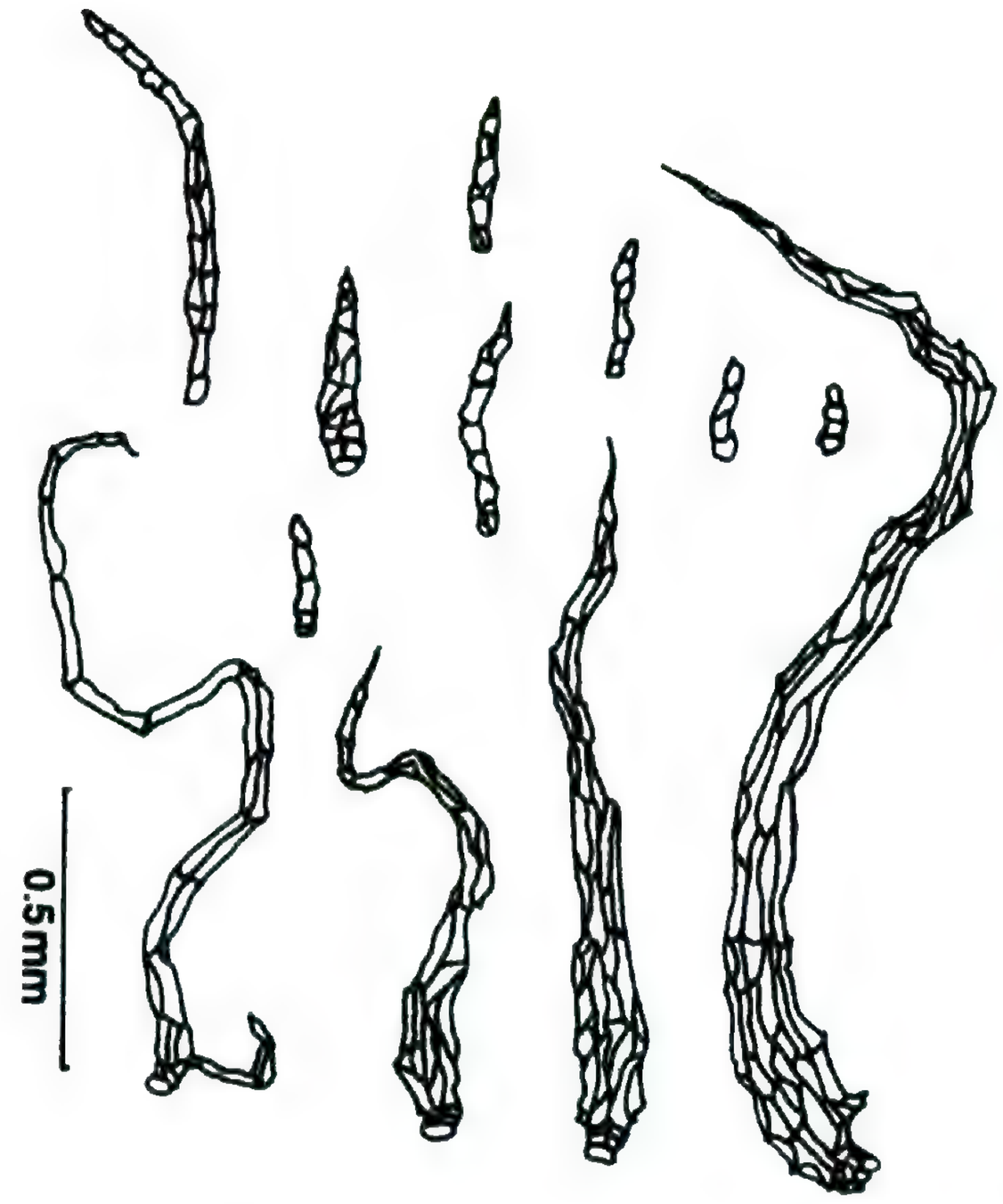


Figure 3. Representative laminar scales from a single leaf of *Phanerophlebia auriculata* (*Yatskievych et al. 83–10*).

protected habitats in which these plants usually grow.

The most highly developed scales occur along the proximal portions of the petioles and on the rhizomes. The rhizome and largest petiolar scales are similar in morphology within most species, but the rhizome scales are usually less variable and often slightly smaller and more densely ciliate along their margins than those of adjacent petiole bases. The largest rhizome and petiolar scales range in length from 2.5–4.0 mm in *P. gastonyi* to 10–15 mm in *P. macrosora*. Rhizome scales are ovate to elliptic-lanceolate, but petiolar scales vary from linear to ovate in most species, due to the gradation of mixed scale types described above. Exceptions are *P. gastonyi*, which has very few narrower scales mixed with the sparse, ovate scales along the petiolar bases, and *P. pumila*, which has only linear-filiform petiolar scales except in the very basal portions.

The margins of the rhizome and petiolar scales are ciliate, and those of *Phanerophlebia macrosora* are strongly erose-ciliate. In all taxa, there is a tendency for these cilia to break off with age. In *P. nobilis*, cilia tend to be abraded easily, and a diligent search with a dissecting microscope is necessary to observe the few remaining on scales at rhizome or leaf maturity. In contrast, the margins of petiolar scales in *P. gastonyi*, *P. juglandifolia*, and *P. macrosora* tend to remain relatively unaltered at maturity, although the cilia become abraded with age. The petiole bases of young leaves in all species are covered with a dense indument of imbricate scales except in *P. gastonyi*, wherein the scales are sparser and essentially non-overlapping. In *P. macrosora*, the dense, chaffy covering of scales is especially persistent, even with age.

Rhizome and petiolar scales are concolorous, except in *Phanerophlebia gastonyi* and *P. juglandifolia*. The former species has scales with broad, dark centers of sclerified cells and narrow, hyaline margins. In the latter species the darker, central band is of variable width, though well defined from the correspondingly broader, hyaline margins. Specimens of *P. macrosora* rarely have scales with slightly darker, poorly differentiated, central regions. Otherwise scales of this species are light tan. The remaining taxa produce tan to orange-brown scales; those of *P. nobilis* and *P. umbonata* are usually a pronounced orange-brown in color.

Hybridization and Polyploidy

Chromosome counts for *Phanerophlebia* species are presented in Table 1. These indicate that the base number for the genus is $x = 41$, a common number in the Dryopteridaceae. Representative chromosome counts had been published previously for most species and appeared to indicate a relatively simple cytological situation in the group, with less polyploidy and hybridization than is typical in *Polystichum* and other related genera. The earliest reports for the genus were diploid counts for *P. umbonata* (Wagner, 1963; Mickel et al., 1966). Diploid counts had also been published for *P. juglandifolia*, *P. macrosora*, *P. nobilis*, and *P. remotispora* (Smith & Mickel, 1977). Two tetraploid taxa had been identified, *P. auriculata* (Reeves, 1978) and *P. pumila* (Smith & Mickel, 1977), and except for a single tetraploid count for a sample tentatively ascribed to the otherwise diploid *P. nobilis* var. *remotispora* (Smith & Mickel, 1977, reported as *P.* cf. *remotispora*), there was no evidence of cytological heterogeneity in any of the species. The only presently accepted species for which no chromosome count exists is *P. haitiensis*, which is known historically from very few collections and is presumed extinct at its type locality in Haiti.

New counts reported in Table 1 agree with most earlier counts for the genus, but document the surprising find that *Phanerophlebia juglandifolia*, as traditionally circumscribed, comprises two cytotypes (Yatskievych & Gastony, 1987). The previously published count from Oaxaca, Mexico (Smith

Table 1. Chromosome numbers in *Phanerophlebia*. All counts are from meiotic material. Vouchers for new counts are accessioned at IND and MO, with duplicates to be distributed elsewhere.

Species	Number of Meiotic Bivalents	Source
P. auriculata	82	U.S.A. **Arizona:** Chochise Co., Bass Canyon, Galiuro Mtn., 3 Jan. 1983, *Yatskievych et al. 83-10*; Garden Canyon, Huachuca Mtn., 17 May 1983, *Yatskievych 83-161*; Santa Cruz Co., Sycamore Canyon, Pajarito Mtn., 30 Dec. 1982, *Yatskievych & Yatskievych 82-273*; Yavapai Co. (Reeves, 1978). **New Mexico:** Dona Ana Co., Ice Canyon, Organ Mtn., 21 July 1984, *Yatskievych et al. 84-68.*
P. gastonyi	41	MEXICO. **Chiapas:** ca. 13 km N of Berriozabal, 17 July 1985, *Yatskievych et al. 85-182.* **Oaxaca:** (Smith & Mickel, 1977, as *P. juglandifolia*). **Veracruz:** 1 km N of Pas de Enriquez on rd. from Jalapa to Misantla, 29 Sep. 1986, *Yatskievych & Gastony 86-337.*
P. juglandifolia	82	MEXICO. **Chiapas:** (Smith & Mickel, 1977, as *P.* cf. *remotispora*). COSTA RICA. **San José:** 6 km S of Hwy. 2 on Hwy. 12 to Santa María de Dota, 15 Mar. 1986, *Yatskievych & McCrary 86-13.* **Heredia:** 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, *Yatskievych & McCrary 86-31.*
P. juglandifolia × *macrosora*	123I	COSTA RICA. **Heredia**: 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, *Yatskievych & McCrary 86-31a.*
P. macrosora	41	COSTA RICA. **Heredia:** 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, *Yatskievych & McCrary 86-30.* MEXICO. **Oaxaca:** trail to Llano Verde, 1–2 mi. NE of Natividad, 30 Dec. 1983, *Yatskievych et al. 83-467*; 22 mi. NE of Teotitlán del Camino on rd. to Huautla, 28 Sep. 1986, *Yatskievych & Gastony 86-329*; (Smith & Mickel, 1977).
P. nobilis		
var. *nobilis*	41	MEXICO. **México:** 1–2 km E of San Rafael on W slope of Volcán Iztaccihuatl, 21 July 1985, *Yatskievych et al. 85-211.* **Oaxaca:** 35 km S of Tlaxiaco on Hwy. 125 to Putla, 27 Sep. 1986, *Yatskievych & Gastony 86-327;* (Smith & Mickel, 1977, as *P. nobilis*).
var. *remotispora*	41	MEXICO. **Chiapas:** ca. 13 km N of Berriozabal, 17 July 1985, *Yatskievych et al. 85-186*; (Smith & Mickel, 1977, as *P. remotispora*). **Hidalgo:** 17 mi. SW of Chapulhuacan on Hwy. 85, 4 May 1983, *Yatskievych & Wollenweber 83-128*; 32 km SW of Tamazunchale on Hwy. 85 to Jacala, 22 Dec. 1983, *Yatskievych et al. 83-353.* **Veracruz:** ca. 3 km SW of Orizaba on Hwy. 150D, Sierra de San Cristobal, 9 May 1983, *Yatskievych & Wollenweber 83-158.*
P. pumila	82	MEXICO. **Chiapas:** (Smith & Mickel, 1977). **Oaxaca:** Llano de Las Flores, at high point on Hwy. 175 N of Ixtlán de Juarez, 13 July 1985, *Yatskievych et al. 85-139*; NE of Ixtlán de Juarez on old rd. from Capulalpan de Mendez, near junction with newer road to Francisco I. Madero, 19 July 1985, *Yatskievych & Gonzalez L. 85-209*; (Smith & Mickel, 1977).
P. umbonata	41	MEXICO. **Nuevo León:** SW of Monterrey on rd. to Valle de San Angel, lower slopes of Mesa de Chipinque, 1 May 1983, *Yatskievych & Wollenweber 83-87*; km post #29 on Hwy. 58 from Linares to San Roberto, 19 Dec. 1983, *Yatskievych et al. 83-299*; Cola de Caballo, W of El Cercado, ca. 20 mi. S of Monterrey, 4 Jan. 1984, *Yatskievych et al. 84-04*; Cañon de San Francisco, Sierra Madre Oriental, ca. 35 km SE of Monterrey, 16 Sep. 1986, *Yatskievych & Gastony 86-250.* **San Luis Potosí**: (Mickel et al., 1966). U.S.A. **Texas:** Brewster Co., Maple Canyon, Basin, Chisos Mtn., 12 Mar. 1985, *Yatskievych & McCrary 85-05.*

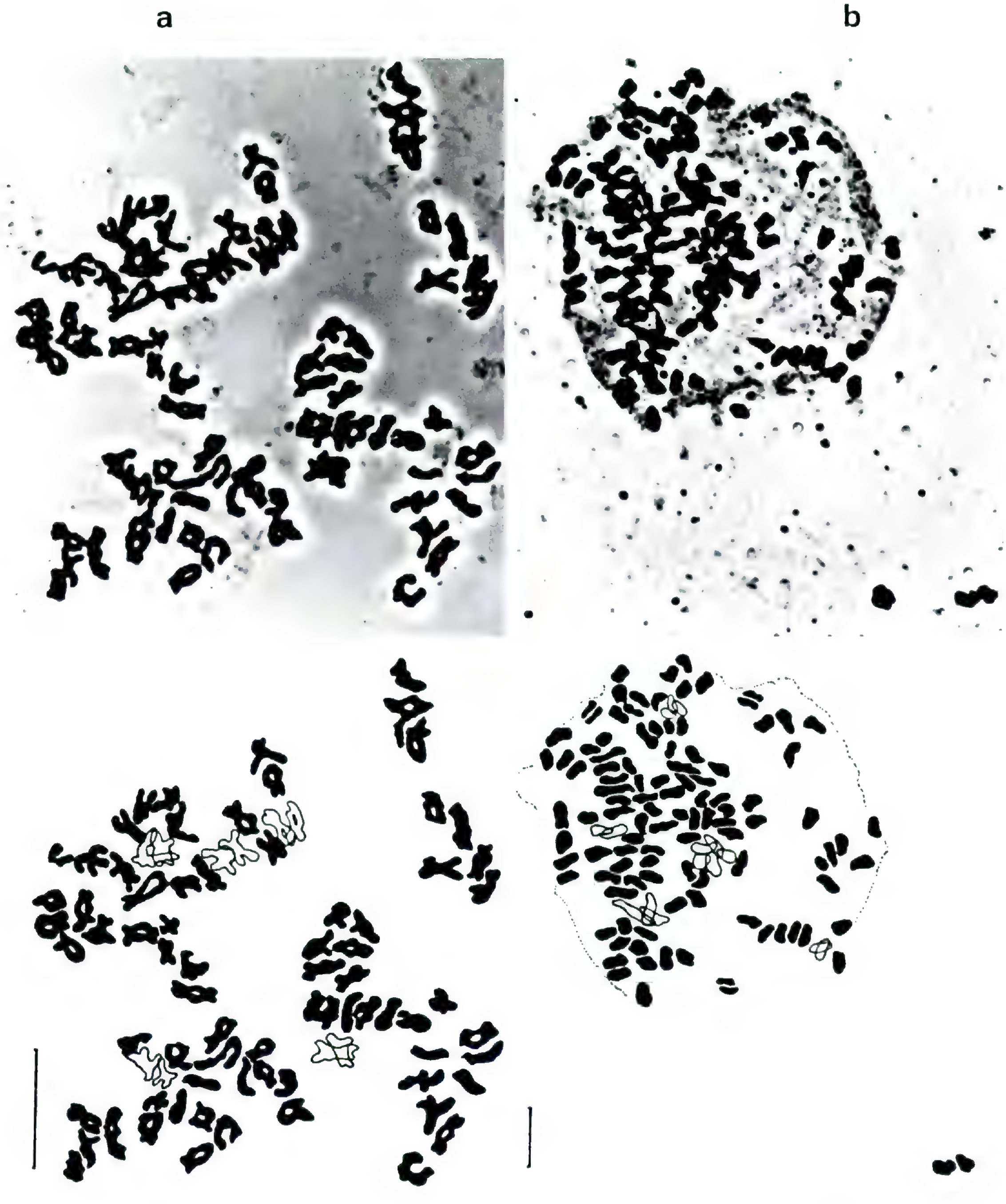


Figure 4. Meiotic preparations illustrating new chromosome counts in *Phanerophlebia*. a, b, photographs; a′, b′, interpretive camera lucida drawings. —a. *P. juglandifolia*, $2n = 82$ II (*Yatskievych & McCrary 86–13*). —b. *P. juglandifolia* × *macrosora*, $2n = 123$ I (*Yatskievych & McCrary 86–31a*). Scale bars = 10 μm.

& Mickel, 1977), applies to the rare diploid taxon treated as *P. gastonyi* in the present work, whereas the tetraploid count attributed to *P.* cf. *remotispora* by Smith and Mickel (1977) applies to the taxon (Fig. 4) treated herein as *P. juglandifolia* sensu stricto. A further novelty was the documentation of sterile triploid hybrids (Fig. 4) in a mixed population of diploid *P. macrosora* and tetraploid *P. juglandifolia*, the only known primary hybrid in the genus. Thus the cytological situation in this small

group is somewhat more complex than was suggested by earlier studies.

As has been noted above, spore size did not prove to be a reliable indicator of ploidy in *Phanerophlebia* and was useful only in discriminating *P. gastonyi* from its relatives. However, the variability of spores in the small sample of *P. haitiensis* and the apparent high number of malformed spores in this taxon suggest that hybridization and/or polyploidy may have had a role in its formation.

Measurements of epidermal cells were also somewhat equivocal as a means of documenting polyploidy in the genus. Epidermal cells in *Phanerophlebia* species are irregular in size and shape, but are extremely wavy-margined (jigsaw-puzzle-piece shaped) in surface view (Fig. 5). Stomates are restricted to the abaxial surface of the pinnae and are more or less of the polocytic type (sensu Van Cotthem, 1970). Although polyploids, such as *P. pumila,* generally possess larger epidermal cells on both adaxial and abaxial pinna surfaces, the within-sample variation is so high that quantification of these measurements was useless. Measurements of stomates (technically, guard cell lengths) proved to be a more stable means of distinguishing diploid taxa (mean 47.7 μm, range 44.9–54.3 μm) from polyploids (mean 60.8 μm, range 59.6–63.7 μm). Measurements from a cleared pinna of *P. haitiensis* (Fig. 5) fell within the range of guard cell size in polyploid taxa, a further suggestion that this species is a polyploid of some sort.

A brief discussion summarizing what is known about each of the four polyploids in the genus (including *Phanerophlebia haitiensis*), along with speculations as to the likely parentage of each, is presented below. The sterile triploid, *P. juglandifolia* × *macrosora,* is included in the discussion of *P. juglandifolia.*

Phanerophlebia auriculata. This tetraploid occupies the northwestern portion of the range of the genus (Fig. 6). Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have indicated that it is probably an allopolyploid, but did not result in any firm conclusion regarding potential progenitors within the genus. These data are, however, consistent with the speculations that follow. Analysis of chloroplast DNA restriction site mutations (Yatskievych et al., 1988) suggested that one of its parental species is *P. nobilis.* Morphologically, *P. nobilis* var. *nobilis* and *P. auriculata* are very similar, and the rare occurrence of acroscopically auriculate pinnae in *P. nobilis* (otherwise unique to *P. auriculata*) reinforces this similarity. The other morphologically similar diploid occurring in the northern portion of the generic range is *P. umbonata* (Fig. 6). These taxa all share identical rhizome and petiolar scale types and overall leaf morphology. Specimens from some localities where the ranges of these taxa overlap have been misdetermined by earlier workers and a few samples, such as those collected by Robert Bye in the Sierra Madre of Chihuahua, Mexico (i.e., *Bye 6989, 7094, 7363*), were quite difficult to determine during the present research. *Phanerophlebia auriculata* and *P. umbonata* share a tendency for rhizomes to branch with age, a feature not seen in *P. nobilis.* Biogeographically, the derivation of *P. auriculata* from *P. nobilis* and *P. umbonata* also seems reasonable, given that these three taxa are the only ones known to occur in northern Mexico. However, mixed populations have not been found in nature.

Phanerophlebia haitiensis. As noted above, measurements of stomata suggest that this rare taxon is some sort of polyploid, and its irregular spore size and relatively high number of malformed spores suggest that hybridization is involved. The irregular pattern of anastomosing venation also leads me to suspect that it is of hybrid origin. This taxon is presumed extinct in Haiti (see below, under taxonomic treatment) and was unavailable for laboratory study, so no comparative information is available from cytological, isozymic, or chloroplast genomic studies. What is unusual is that no other species of *Phanerophlebia* has ever been recorded from Hispaniola, making it difficult to imagine how this taxon might be present at a single, isolated site in Haiti.

Morphologically, *Phanerophlebia haitiensis* is reminiscent of *P. nobilis.* The few specimens that exist are intermediate in venation between free-veined variety *nobilis* and reticulate-veined variety *remotispora,* but *P. haitiensis* has smaller leaves and fewer pinnae than is usual for either variety of *P. nobilis.* It is possible that the irregular spores and reduced leaves might have resulted from inhospitable environmental conditions, rather than from genetic causes, but this would not explain the relatively large stomates and the irregularly anastomosing venation. The existence of two morphologically similar collections from Guatemala (*Beaman 3056*) and Honduras (*Moran 5706*) (see under taxonomic treatment) suggests that further fieldwork in southern Mexico and Central America may eventually result in at least partial resolution of the enigma surrounding this taxon.

Phanerophlebia juglandifolia. Yatskievych and Gastony (1987) discussed the two cytotypes constituting the traditional taxon *P. juglandifolia* and ascertained that the type specimen of the name agrees with the tetraploid. Morphological characters

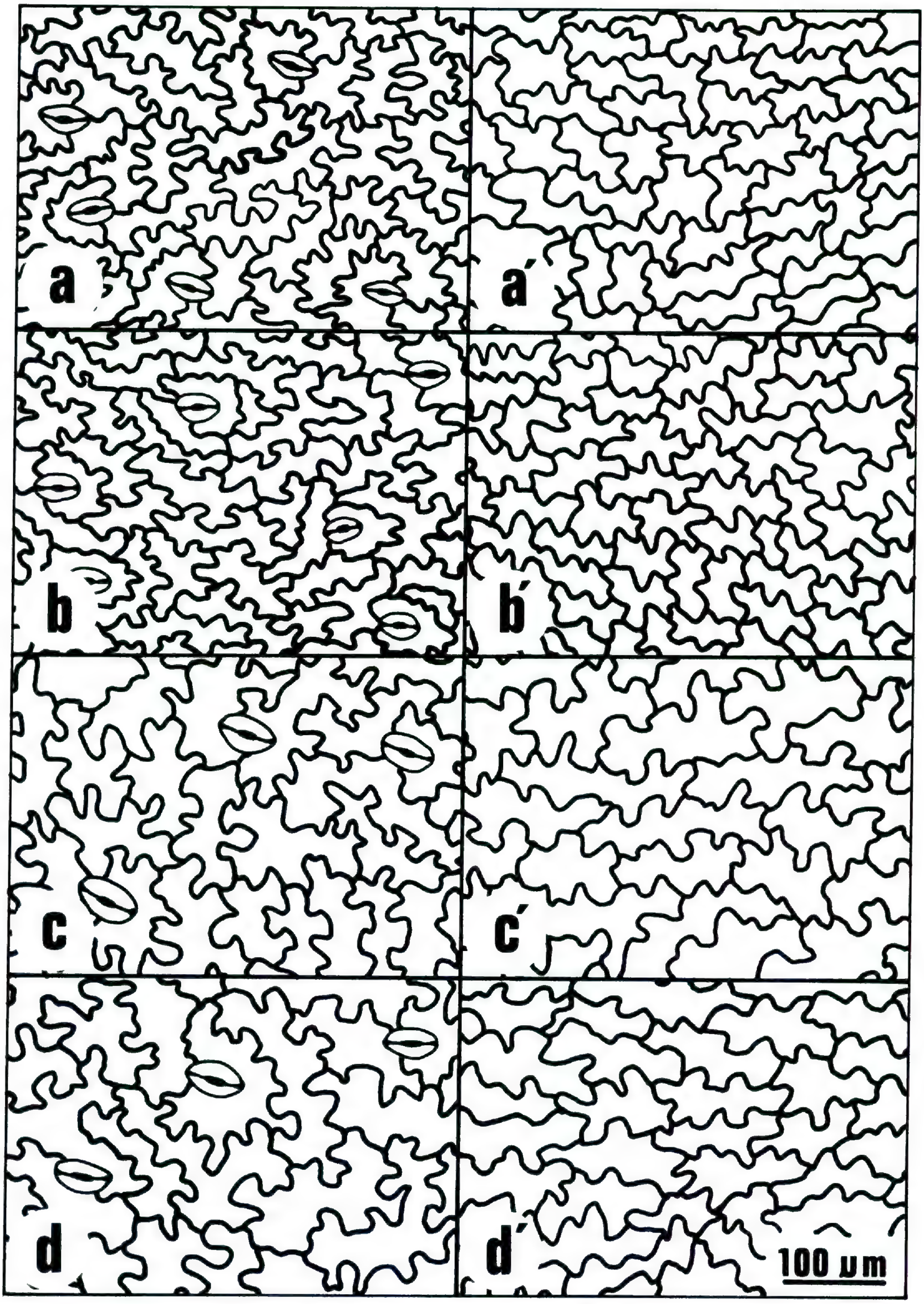


Figure 5. Camera lucida drawings of epidermal cells (surface view) of *Phanerophlebia* species. a–d, abaxial surfaces, with stomates; a′–d′, adaxial surfaces. —a. *P. gastonyi* (*Yatskievych et al. 85–182*). —b. *P. nobilis* var. *remotispora* (*Yatskievych & Wollenweber 83–158*). —c. *P. pumila* (*Mickel 5377*). —d. *P. haitiensis* (*Ekman 7793*).

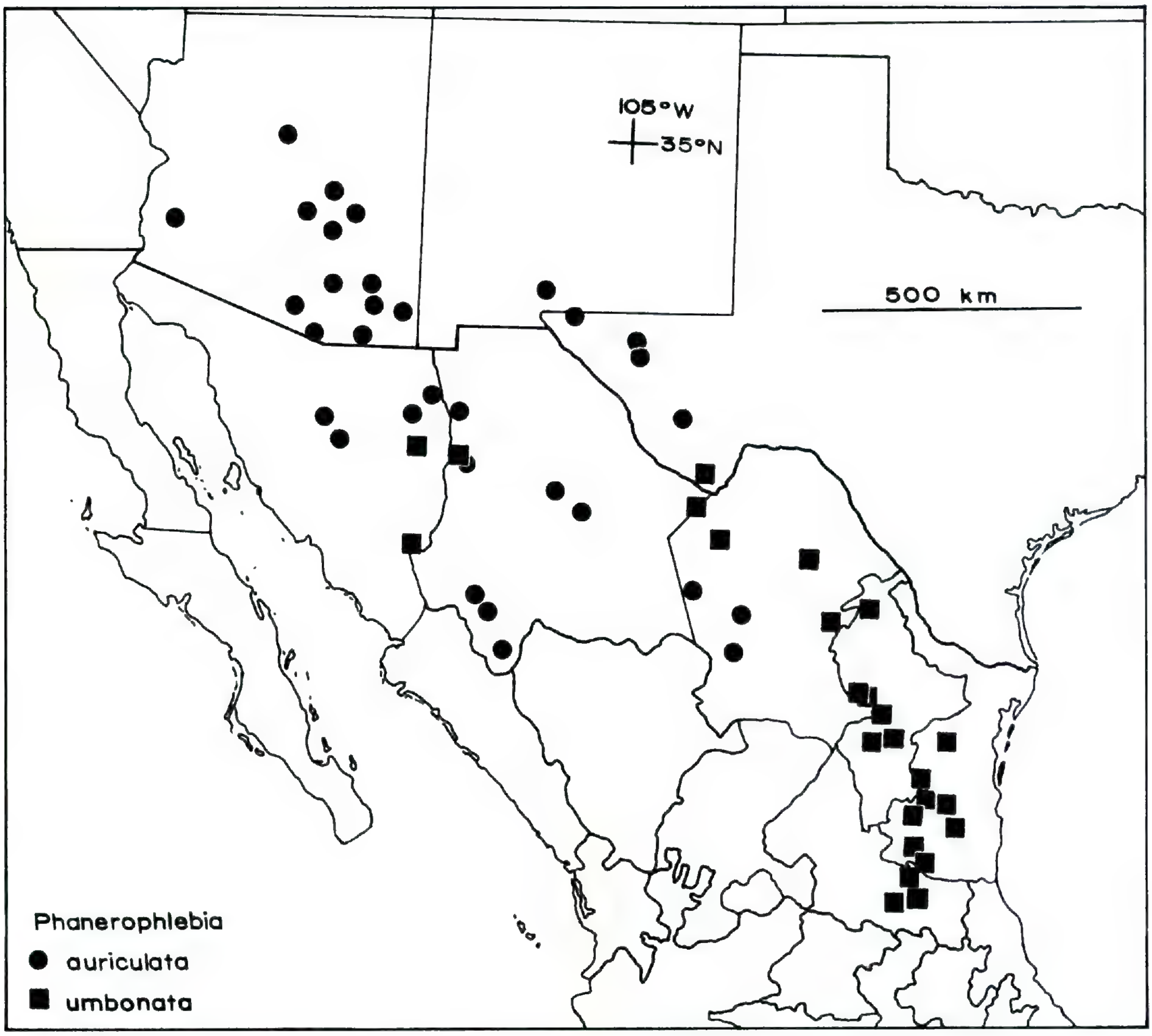


Figure 6. Distributions of *Phanerophlebia auriculata* and *P. umbonata*, based upon herbarium specimens examined.

that separate tetraploid *P. juglandifolia* sensu stricto from the diploid here treated as *P. gastonyi* are detailed below in the taxonomic treatment. Restriction site analysis of the chloroplast genomes (Yatskievych et al., 1988) of these plants confirmed that the diploid plants formerly attributed to the species were a progenitor of the tetraploid. Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) of the tetraploids showed high levels of fixed heterozygosity not segregating in their gametophytic offspring, which is consistent with the hypothesis that these plants are of allopolyploid origin. The identity of the other parental taxon unfortunately remains unclear, particularly because the isozyme studies did not supply convincing evidence for the identity of the second progenitor taxon. The possibilities for the second parent include: (a) *P. nobilis* var. *remotispora*, the other net-veined taxon in the genus; (b) a free-veined taxon, such as *P. macrosora*; or (c) a parental taxon that is now either extinct or has not been sampled. Of these three hypotheses, the first, that *P. nobilis* is involved in the parentage of *P. juglandifolia*, seems the least likely. Morphologically, the tetraploids do not combine the critical features of *P. nobilis* and *P. gastonyi*, including rhizome and petiolar scale shape and color and the pattern of spinulose serrulations along the pinna margins. The third hypothesis, of an extinct or at least as yet unsampled progenitor taxon, may be the most likely, but cannot be evaluated from the present data. The other hypothesis, that a free-veined, indusiate species of *Phanerophlebia* contributed the other parental genome to *P. juglandifolia*, was explored by Yatskievych and Gastony (1987). Surprisingly, of the other extant species in the genus, the one that possesses the most likely morphology to account for the differences between *P. juglandifolia* and *P. gastonyi* is *P. macrosora*.

The tetraploid possesses rhizome and petiolar scales with color, shape, and size somewhat intermediate between *P. gastonyi* and *P. macrosora*, and its pinna size, shape, and number are also plausible for this cross (Yatskievych & Gastony, 1987; see also below, under taxonomic treatment). However, *P. juglandifolia* bears a far closer superficial resemblance to *P. gastonyi* than to *P. macrosora*, and lacks the pronounced odor, coarsely serrate pinna margins, and geniculate petiolar bases that characterize the latter species.

Compounding the problem of establishing the parentage of *Phanerophlebia juglandifolia* is the existence of rare, naturally occurring, triploid hybrids between this species and *P. macrosora* (Table 1, Fig. 4) from Costa Rica (see also below, under taxonomic treatment). These hybrids, which produce aborted spores and are therefore sterile, are of intermediate morphology between *P. juglandifolia* and *P. macrosora* and were relatively common at the single site where I was able to observe them. If tetraploid *P. juglandifolia* contained one genome from *P. gastonyi* and the other from *P. macrosora*, then the Costa Rican hybrids would represent a backcross and should display 41 bivalents and 41 univalents at diakinesis. Instead, the triploids display 123 univalents (Table 1). Unfortunately, this weakens the argument that *P. macrosora* might have been the second progenitor of *P. juglandifolia*. The derivation of this tetraploid thus remains unresolved.

Phanerophlebia pumila. This morphologically reduced tetraploid remains enigmatic. Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) indicate that it is probably of allopolyploid origin, as are other tetraploids in the genus, but do not assist in determining its parentage. Surprisingly, its pattern of chloroplast DNA restriction fragments (Yatskievych et al., 1988) do not support any of the extant species of *Phanerophlebia* as a likely progenitor. Thus, the experimental evidence suggests that one or even both parental diploids of this taxon are either extinct or so rare as not to have been sampled by collectors thus far. Potential progenitors are to be sought in the mountains of southern Mexico and adjacent Guatemala, where overall species diversity within the genus is the highest.

The Wagner parsimony analysis of the molecular data (Yatskievych et al., 1988) grouped *Phanerophlebia pumila* and *P. umbonata* as sister taxa. It therefore suggested that the latter species might be involved in the parentage of *P. pumila*. This seems unlikely biogeographically, because the two are widely allopatric. *Phanerophlebia pumila* displays none of the critical morphological features of *P. umbonata*, such as a tendency for branching rhizomes or umbonate indusia. Instead, based upon a qualitative assessment of morphological characters, it seems at least plausible that *P. nobilis* might rather have contributed one of the genomes to form *P. pumila*. Although the leaves of *P. pumila* tend to be highly reduced in size and pinna number, and the petiolar scales are at most linear-filiform, the pinna shape and the rhizome scales, as well as the overall leaf shape, suggest some depauperate samples of *P. nobilis*. Further, this diploid can sometimes occur in sinkholes and other habitats normally associated with *P. pumila*, and one set of replicate herbarium specimens examined during this study (*Hinton 12428*) consisted of a mixed collection of these two species. No other species of *Phanerophlebia*, except the northern tetraploid, *P. auriculata*, has been found in the specialized habitat type (sheltered, overhanging rock walls) to which *P. pumila* is restricted.

Phylogenetic Relationships

Most modern systematists agree that questions of phylogeny are best approached through consideration of the shared, derived characters (synapomorphies) present in various subsets of species within a clade. Such analyses require several assumptions to be accepted. First, the group in question should be monophyletic. Second, it is assumed that character states for various features can in some way be polarized; that is, that there is a rational way to distinguish apomorphies (derived character states) from plesiomorphies (primitive character states). Finally, the researcher must assume that he or she can detect homoplasy (parallel or convergent evolution), which will tend to confuse interpretation of any analysis.

There is little doubt that the species of *Phanerophlebia* are monophyletic. However, the species are so character-poor that although autapomorphies (derived characters unique to one taxon) allow separation of the species from one another, as in the key to species below, there are virtually no synapomorphies that can be documented. Further, those character states that are shared by two or more taxa, such as the rhizome and petiolar scale type of *P. nobilis* and *P. umbonata* (among the diploids), are not easily polarized. Also, it is apparent from study of independent data sets (such as restriction site analysis of the chloroplast genomes) that some characters judged by most earlier workers to be important for classification in the group, particularly the anastomosing venation patterns of *P. gastonyi* and *P. nobilis* var. *remotispora*, are homoplasious.

Thus, no formal cladistic analysis of morphological characters is attempted here.

Generic Considerations

The genus *Phanerophlebia* was first erected by Presl (1836), based on *Aspidium nobile* Schltdl. & Cham. Presl (1836) also described *Amblia*, based on *Polypodium juglandifolium* Humb. & Bonpl. ex Willd., and *Cyrtomium*, based on *Polypodium falcatum* L. f. As with many of Presl's genera, acceptance of these innovations was neither immediate nor unanimous, and various authors have treated the groups differently up to present times. Smith (1842) first submerged *Amblia* (which Presl had allied with *Polypodium* L.) in *Phanerophlebia* (which Presl had allied with *Aspidium* Sw.), while maintaining this genus separate from *Cyrtomium*, and recognizing the relationship of both to *Polystichum* Roth. Moore (1857) was the first to unite *Phanerophlebia* and *Cyrtomium*, under the latter name, but retained two subgroups based on the two genera. Diels (1899) presented the most extreme alternative to Presl's segregate genera by submerging *Amblia*, *Cyrtomium*, and *Phanerophlebia* in his large and heterogeneous version of *Polystichum*. Since that time, most pteridologists have either maintained *Phanerophlebia* as a separate genus (e.g., Underwood, 1899; Maxon, 1912) related to *Polystichum*, or have included *Phanerophlebia* in an expanded concept of *Cyrtomium* (e.g., Morton, 1957; Tryon & Tryon, 1982).

No recent workers have questioned the close relationship of *Phanerophlebia* and *Cyrtomium* to *Polystichum*. In fact, one New World taxon, *Polystichum dubium* (Karsten) Diels, of Andean South America and adjacent Central America, continues to be placed in *Cyrtomium* by some authors (e.g., Tryon & Stolze, 1991). Although superficially similar to some *Cyrtomium* and *Phanerophlebia* species, this morphologically variable taxon does not appear to be a geographically disjunct member of either group, and is known to hybridize with *Polystichum platyphyllum* (Willd.) C. Presl in Ecuador (Barrington, 1985). Its classification within *Polystichum* was beyond the scope of the present work, and it remains to be studied in greater detail in the future.

Two hypotheses have been suggested to account for the presence of two morphologically similar "splinter genera" in the Old and New Worlds. Christensen (1930) regarded *Phanerophlebia* and *Cyrtomium* as independent derivatives from different polystichoid ancestors. By this reasoning, the strong similarities between the two groups would reflect convergent evolution, i.e., homoplasy. In contrast, Copeland (1947) suggested a single, Asiatic origin for the entire group, with an American component having become established via a transoceanic, disjunctional event. He noted that such a major disjunctional pattern exists in a few other fern genera, such as *Plagiogyria* (Kunze) Mett. (Plagiogyriaceae), and this scenario is therefore plausible.

Evidence in support of Christensen's (1930) hypothesis comes from several sources. An interesting general observation concerns the distribution of apogamous taxa in the polystichoid ferns. Several authors have remarked on the exceedingly large number of apomictic taxa that have been described in *Cyrtomium* (e.g., Shing, 1965) and *C. falcatum* was the subject of classic studies on the phenomenon of apogamy in ferns (Manton, 1950). Examination of the scant information available on apogamy in Asiatic *Polystichum* (Tsai & Shieh, 1985) indicates that this phenomenon also occurs in scattered species within the Asiatic component of the genus. In contrast, as noted above, all fertile taxa of *Phanerophlebia* reproduce sexually. This is also true of all species of American *Polystichum* that have been examined. Although hybridization and polyploidy are relatively common throughout *Polystichum*, apomixis is expressed only in the Old World contingent.

The morphological innovations said to unite *Phanerophlebia* and *Cyrtomium* do not survive close scrutiny. Mitsuta (1977), who studied venation patterns in polystichoid ferns, noted that the areolae in *Phanerophlebia* were narrower (i.e., elongate, with more acute ends) than those in *Cyrtomium* and lacked well differentiated, free, included veinlets as are found in most species of the latter group. Wagner (1979), in a summary of reticulate veins as systematic characters, also noted that the pattern of anastomoses develops differently in the two genera. In *Phanerophlebia*, anastomoses are of a submarginal ontogenetic type, which Wagner (1979) termed "discal," but in *Cyrtomium* they are "costal" in origin.

Patterns of perispore deposition were said by Tryon and Tryon (1982) to be identical in *Phanerophlebia* and *Cyrtomium*. Superficially, the two groups appear similar, but in *Phanerophlebia* species the surface between the inflated folds is smooth to rugulose and imperforate. However, in the seven species representing *Cyrtomium* that I studied, the outer perispore surfaces were not only rugulose, but also had few to many microperforations (Fig. 7).

Other evidence for the separate origins of *Phanerophlebia* and *Cyrtomium* comes from a phylogenetic analysis of restriction site mutations in the chloroplast genomes of the two genera (Yatskievych

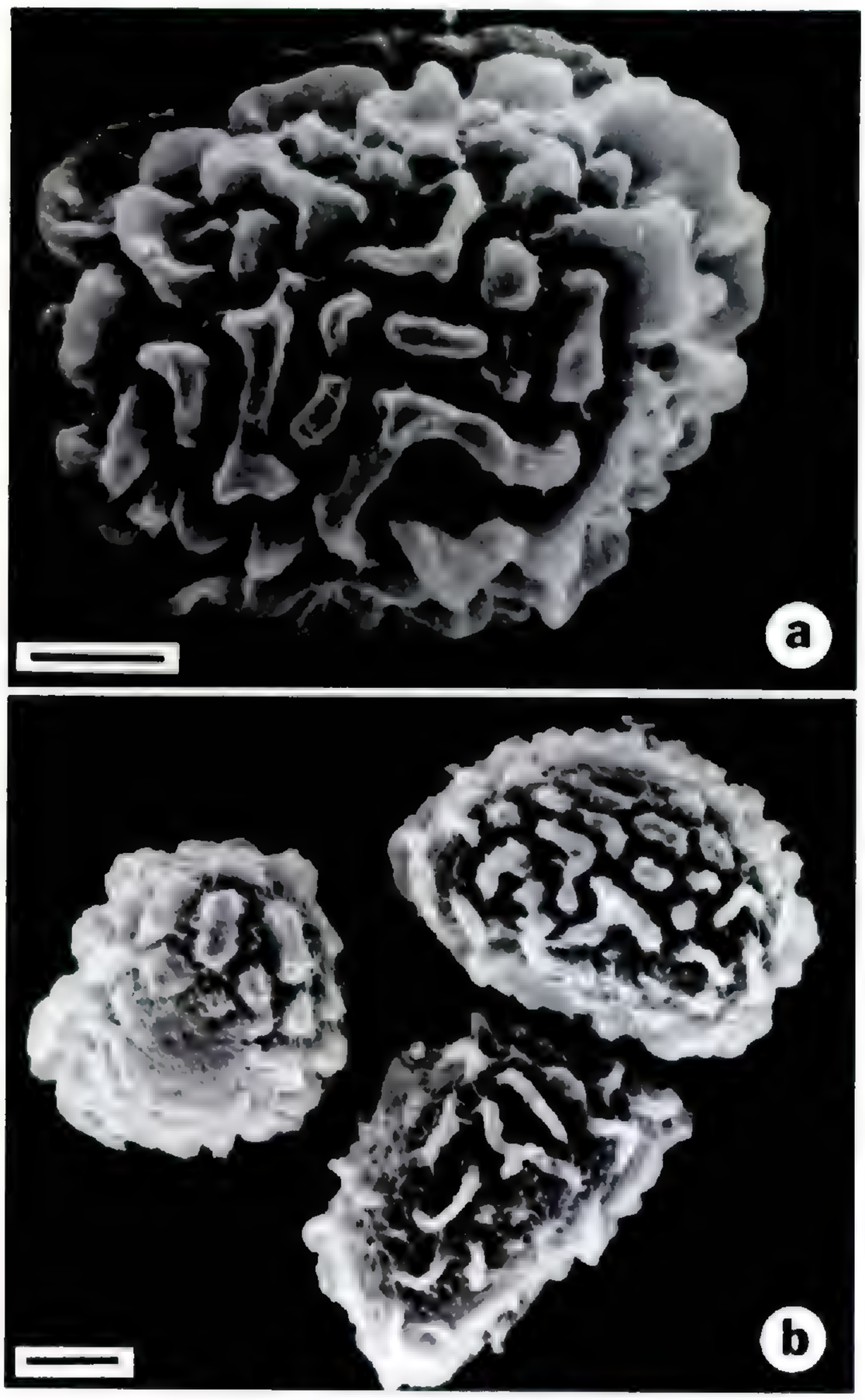


Figure 7. Spores of *Cyrtomium* species. —a. *C. macrophyllum* (*Mitsuta* s.n.), with the very few microperforations between the folds not easily seen. —b. *C. falcatum* (*Yatskievych & McCrary 83–184*), the microperforations more easily seen. Scale bars = 10 μm.

et al., 1988). In that study, the groups of *Phanerophlebia* and *Cyrtomium* species were less related to one another than either was to a group of taxa representing *Polystichum*.

Although present evidence supports the hypothesis that *Phanerophlebia* and *Cyrtomium* were independently derived from different ancestral groups, the real question that remains unanswered is whether either of these derivatives is distinct enough to merit recognition as a genus separate from *Polystichum* (Wagner, 1985). Yatskievych (1989) suggested that simplification of leaf dissection is a trend that has occurred repeatedly in different species groups throughout *Polystichum*. Taken singly, all of the characters said to separate *Phanerophlebia* or *Cyrtomium* from *Polystichum* also occur in other species of that genus.

The venation patterns in two other Asiatic segregates of *Polystichum*, *Cyrtogonellum* Ching and *Cyrtomidictyum* Ching, actually resemble those of *Phanerophlebia* far more closely than do those of *Cyrtomium*. However, Ching (1938, 1957) clearly differentiated these segregate genera from *Phanerophlebia*, *Cyrtomium*, and *Polystichum*, based on other morphological innovations they possess. Species in both groups also have been submerged in *Polystichum* by some subsequent authors (e.g., Kramer et al., 1990).

Perispore pattern was cited by Tryon and Tryon (1982) as a stable character for separation of *Cyrtomium* (including *Phanerophlebia*) from *Polystichum*. These authors felt that the simpler, imperforate perispore lacking columellae of *Cyrtomium* was more like that found in *Dryopteris* than the perforate or reticulate, often columellate formation characteristic of *Polystichum*. Although the perispores found in *Cyrtomium*, *Phanerophlebia*, and *Dryopteris* are remarkably similar, two factors argue against placing too much emphasis on this interpretation. First, as noted above, at least some species of *Cyrtomium* possess a perispore with microperforations (Fig. 7). Second, *Polystichum* contains species with a broad range of perispore types. Mitui (1973) attempted to classify the perispore types found in 40 species of *Polystichum*. He differentiated eight perispore types, based on differences in patterns of ornamentation. Most of the species studied had reticulate or perforate perispores of varying complexity, but a small group possessed what Mitui felt to be a derivative perispore type closely related to that of *Cyrtomium* (Figs. 7, 8).

Polystichum species with imperforate perispores are apparently present in both the Old World and New World, although few American taxa have been examined in detail. For example, the perispore type found in *Polystichum lemmonii* Underw. (Fig. 8), of the western United States, is quite similar to that of *Phanerophlebia* species in its relatively compact, imperforate outer layer. As noted above, the widely scattered papillae on the inner perisporal layer of *Phanerophlebia* species also may represent reduced remnants of earlier columellae. Further studies involving a large number of tropical American species of *Polystichum* are needed to resolve the present ambiguities in our knowledge of perispore evolution in the group.

It is probable that *Phanerophlebia* and *Cyrtomium* will eventually be resubmerged in *Polystichum*. In a phylogenetic sense, recognition of these and other splinter genera results in a paraphyletic *Polystichum*, a situation clearly to be avoided. The decision to continue treating *Phanerophlebia* as a separate genus in the present work was a difficult one and stems from my hesitancy in resubmerging a clearly monophyletic unit back into the poorly re-

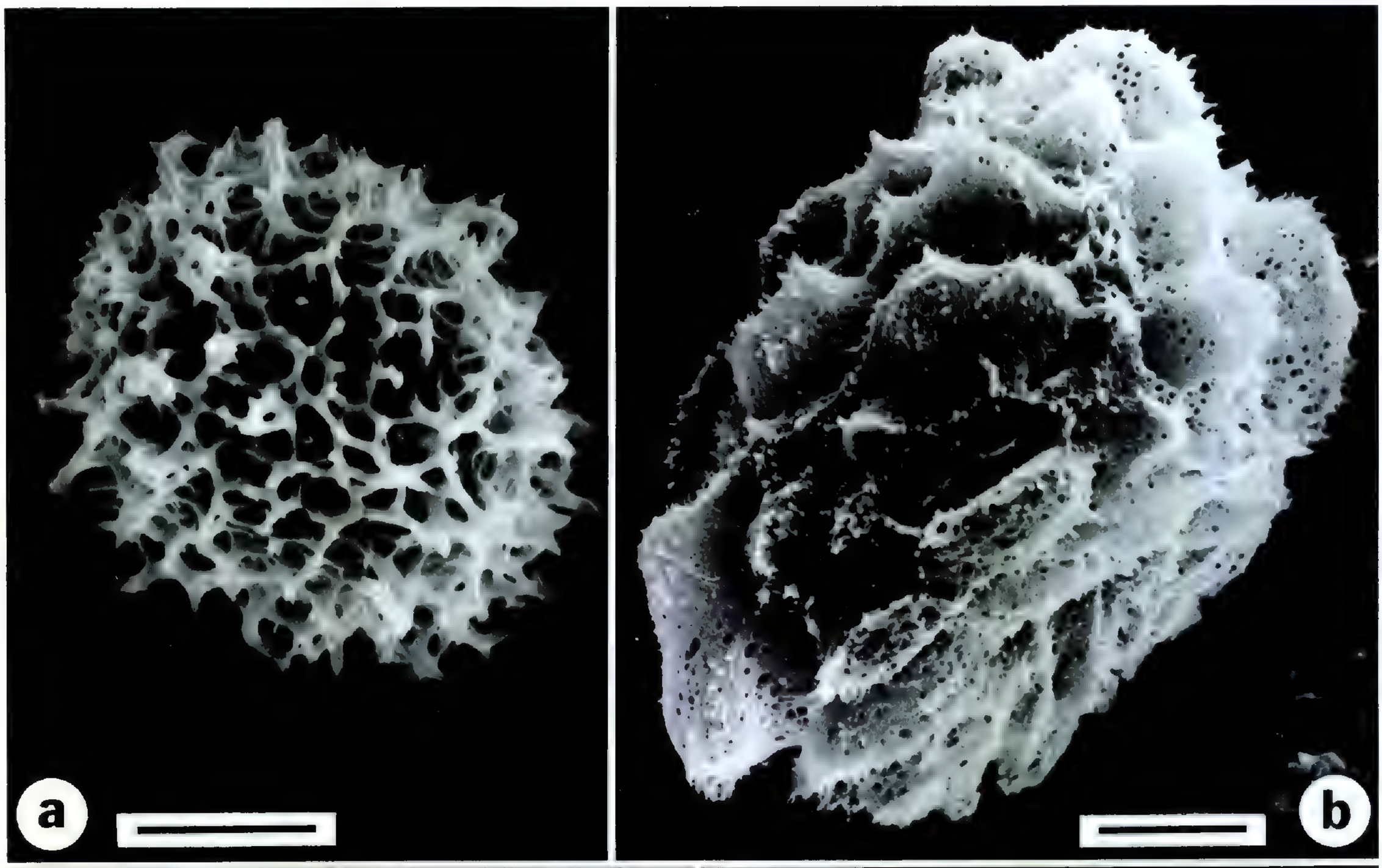


Figure 8. Spores of *Polystichum* species. —a. *P. lonchitis* (*Darrow et al. 2482*), showing the reticulate perispore commonly associated with the genus. —b. *P. munitum* (*Yatskievych & McCrary 84–126*), with a cristate-microperforate perispore. —c. *P. lemmonii* (*D'Arcy 2686*), with a perispore type similar to that found in *Phanerophlebia* and *Cyrtomium*. —d. *P. lemmonii* (*D'Arcy 2686*), abraded spore, showing smooth exine, rugulose inner perispore, and outer perispore with inflated folds. Scale bars = 10 μm.

solved quagmire that represents our present, limited knowledge of classification in *Polystichum*. Particularly in tropical America, *Polystichum* comprises a diversity of species clusters whose interrelationships have not been studied in detail. We not only do not know which of these species clusters is most closely related phylogenetically, or even morphologically, to the *Phanerophlebia* cluster, but we do not have a clear idea how to polarize the states for the various morphological and other characters separating these groups. Because no stable infrageneric classification, similar to that of

Daigobo (1972) for Japan, presently exists for the New World species, it seems most prudent to avoid publishing the new combinations necessary to incorporate all of the presently recognized taxa of *Phanerophlebia* into *Polystichum*.

Taxonomic Treatment

Phanerophlebia C. Presl, Tent. Pterid. 84, 1836. TYPE: *Phanerophlebia nobilis* (Schltdl. & Cham.) C. Presl (*Aspidium nobile* Schltdl. & Cham.).

Amblia C. Presl, Tent. Pterid. 184, 1836. TYPE: *Amblia juglandifolia* (Humb. & Bonpl. ex Willd.) C. Presl [= *Phanerophlebia juglandifolia* (Humb. & Bonpl. ex Willd.) J. Sm.].

Plants perennial, often long-lived, terrestrial, sometimes growing from soil pockets in rock crevices, or epipetric on rock faces; rhizomes dictyostelic, scaly, short-repent to erect, sometimes branched at maturity, usually covered with persistent petiole bases and adventitious roots; rhizome scales unevenly ciliate, the cilia sometimes shed during maturation; leaves clustered at apex of rhizome, monomorphic, evergreen; petioles shorter than or sometimes longer than laminae, scaly (the scales sometimes shed at maturity), with 4–8 vascular bundles arranged in a ring; laminae 1-pinnate (rarely simple) with conform terminal pinnae, chartaceous to subcoriaceous; rachises and costae usually somewhat scaly with reduced scales, grooved adaxially, the grooves ± confluent at junctions; pinnae asymmetrically subcordate to cuneate at base, sometimes with an acroscopic, basal auricle, spinulose-serrulate along margin, at least distally, ovate to narrowly lanceolate, often somewhat falcate, lacking trichomes, but with reduced, often hairlike scales along veins (these grading into the broader, more typical scales along the rachis and petiole); venation anadromous (this often difficult to observe), pinnate, the veins 1–4-branched, extending ± to margin, free or with 1–3 series of marginal anastomoses; sori terminal or apparently lateral on veins, round, in (1–)2–4 series between costa and margin; indusia absent or present, if present then peltate, with erose margins, persistent at maturity or fugacious; sporangia with 64 spores; spores monolete, dark brown; perispore with prominent, inflated folds; exospore smooth. Chromosome number: $x = 41$.

Key to the Taxa of *Phanerophlebia*

(the rare, sterile hybrid, *P. juglandifolia* × *P. macrosora* is not included, but may key imperfectly to one of its parents)

1a. Veins commonly anastomosing toward the margins, in 1–3 series (less frequent in *P. haitiensis*), these sometimes distributed irregularly.
  2a. Sori indusiate (the indusium shriveling at maturity or fugacious); rhizome and petiole scales concolorous, reddish brown.
    3a. Lateral pinnae (2–)6–17 pairs; pinna margins spinulose-serrulate nearly to base ..... 6b. *Phanerophlebia nobilis* var. *remotispora*
    3b. Lateral pinnae 2–4 pairs; pinna margins spinulose-serrulate only in distal half ..... 3. *Phanerophlebia haitiensis*
  2b. Sori exindusiate; rhizome and petiole scales bicolorous, with darker, sclerotic centers and lighter margins.
    4a. Petiolar scales not overlapping, 4–6 mm long, with broad, dark, sclerotic centers and narrow, hyaline margins; buds absent; spores 30–42 μm long ..... 2. *Phanerophlebia gastonyi*
    4b. Petiolar scales usually overlapping, 6–11 mm long, with dark brown central stripes and lighter margins of about equal width; buds often present on rachis in axils of distal pinnae; spores 41–60 μm long ..... 4. *Phanerophlebia juglandifolia*

1b. Veins free, or with a few, rare anastomoses.
  5a. Lateral pinnae 0–3(–5) pairs; leaves usually <40 cm long; broadest petiolar scales <2 mm wide ..... 7. *Phanerophlebia pumila*
  5b. Lateral pinnae (2–)5–17 pairs; leaves usually >40 cm long; broadest petiolar scales >2 mm wide.
    6a. Petiolar scales stramineous to tan; leaves to 2.7 m long; rhizome scales 10–15 mm long, 5–7 mm wide; plants with an unpleasant, skunklike odor when fresh ..... 5. *Phanerophlebia macrosora*
    6b. Petiolar scales brown or reddish brown (rarely lighter colored with age); leaves to 1.25 m long; rhizome scales 2.5–7.5 mm long, 1–4 mm wide; plants without an unpleasant, skunklike odor when fresh.
      7a. Indusia not shriveled at maturity, ± persistent, with a raised, central projection (umbo) ..... 8. *Phanerophlebia umbonata*
      7b. Indusia shriveled at maturity, often fugacious, flat to concave centrally, not umbonate.
        8a. At least some pinnae with a prominent, acroscopic auricle at base; plants of sheltered soil pockets in rock crevices and ledges of mesic canyons; SW United States to N Mexico ..... 1. *Phanerophlebia auriculata*
        8b. Pinnae rarely auriculate at base; plants of stream banks and forest understory (rarely in sinkholes or rock crevices); nearly throughout Mexico in mountainous areas ..... 6a. *Phanerophlebia nobilis* var. *nobilis*

1. Phanerophlebia auriculata Underwood, Bull. Torrey Bot. Club 26: 212. 1899. *Cyrtomium auriculatum* (Underw.) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Chihuahua: cool, damp cliffs, Mapula Mountains, 17 Oct. 1886, *Pringle 831* (holotype, NY; isotypes, CAS, F, GH, K, LL, MICH, MO, NY, P, UC, US).

Plants not strongly scented; rhizomes to ca. 15 mm diam., deeply seated in substrate, short-repent to ascending, sometimes branched at maturity; rhizome scales 3.5–7.5 mm long, 1–4 mm wide, ovate to elliptic-lanceolate, ciliate, concolorous, brown (rarely lighter colored with age); leaves 10–60(–75) cm long (very short leaves sometimes fertile); petioles shorter than to nearly as long as laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hairlike structures above; pinnae (2–)5–12 pairs, to 9 cm long, ovate to lanceolate, usually falcate, the apex usually attenuate, the base obliquely cuneate to subcordate and usually with a prominent, acroscopic auricle (at least some present on every plant), rarely irregularly incised, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 1–3-branched; sori in 2–4 series between costa and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μm long. Chromosome number: $n = 82$.

Illustrations. See original description; also Dittmer et al. (1954: 38), Knobloch and Correll (1962: 164, pinna), Mickel (1979: 163).

Phanerophlebia auriculata grows in soil pockets in rock crevices (usually granite or quartzite); it is restricted to mesic, sheltered ravines and canyons, in oak and pine-oak forests; 600–2300 m; southwestern United States (Arizona, New Mexico, Texas) and northern Mexico (Chihuahua, Coahuila, Sonora) (Fig. 6). Clausen's (1949) report of this species from Nuevo León was based upon misdetermined specimens of *P. umbonata*.

Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have indicated that *Phanerophlebia auriculata* is an allotetraploid taxon. An examination of chloroplast DNA variation in the genus (Yatskievych, 1988) implicated the diploid *P. nobilis* as one potential parent. Based on morphological characters and distribution, the diploid *P. umbonata* appears to be the most likely extant candidate for the other parent. These three taxa are very similar in details of leaf shape and size, rhizome and petiolar scale shape and coloration, pinna number, and venation. Sterile specimens of the two presumed parents are virtually indistinguishable morphologically. *Phanerophlebia auriculata* shows no tendency toward umbonate indusia, a distinguishing character of *P. umbonata*, but does have a tendency for branched rhizomes, which are common in *P. umbonata*, but not produced in *P. nobilis*. The acroscopically auriculate pinnae of *P. auriculata* are not found in *P. umbonata*, but can be encountered rarely in *P. nobilis*. Small auricles are also encountered commonly in another tetraploid, *P. pumila*, suggesting that this character may arise as a side effect of the combination of parental genomes giving rise to these allopolyploids.

Representative specimens. U.S.A. **Arizona:** Cochise County, short canyon near mouth of Garden Canyon, Huachuca Mountains, *Goodding 162–50* (ARIZ, MICH); Gila County, SE wall of Parker Canyon, Sierra Ancha, *Windham 0109B* (ASC); Graham County, Aravaipa Canyon, in the "Box" below Klondyke, *Phillips & Reynolds 2946* (ARIZ, CAS, GH, US); Maricopa County, north canyons, Superstition Mountains, *Goodding 6146* (ARIZ); Pima County, near the top and on the N side of Mt. Baboquivari, *Gould, Darrow & Haskell 2788* (ARIZ); Santa Cruz County, Sycamore Canyon, Pajarito Mountains, *T. & M. Van Devender s.n.* (ARIZ); Yavapai County, Boynton Canyon, W of Sedona, *Deaver 4788* (ARIZ, ASC); Yuma County, deep narrow canyon, Kofa Mountains, *Goodding & Hinckley F-9-39* (MICH, US). **New Mexico:** Dona Ana County, Ice Canyon, Organ Mountains, *Worthington 7679* (ARIZ, NY, UTEP); Socorro County, Luna Park Campground, San Mateo Mountains, *Reeves et al. 88-1* (NMC). **Texas:** Culberson County, Victorio Canyon, E margin of Sierra Diablo, *Johnston, Wendt & Chiang C. 10728* (CAS, LL); El Paso County, Hueco Tanks, Hueco Mountains, *Waterfall 6635* (GH, MO, NY); Jeff Davis County, Rose Canyon, 15 mi. N of Alpine, *Warnock 21779* (LL). MEXICO. **Chihuahua:** vicinity of village of Majalca, *Correll & Johnston 21772* (LL, US). **Coahuila:** Cañon de Calabasa, Sierra Mojada, *Stewart 2198* (GH, LL). **Sonora:** Cañon de Bavispe, region of Río de Bavispe, *Phillips 546* (ARIZ, GH, MICH, NY).

2. Phanerophlebia gastonyi Yatskievych, Novon 2: 445. 1992. TYPE: Mexico. Chiapas: ca. 13 km NW of Berriózabal, limestone outcrops in evergreen tropical hardwood forest, elevation 1000 m, 15 July 1985, *Yatskievych, González L., Ranker, G. Starr & C. Starr 85–182* (holotype, MO; isotypes, ARIZ, CHAPA, IND, MEXU, NY, UAMIZ, UC).

Plants not strongly scented; rhizomes to ca. 5 mm diam., superficial on substrate, short-repent, not branched at maturity; rhizome scales 2.5–4.5 mm long, 1.5–2 mm wide, ovate to elliptic-lanceolate, ciliate, bicolorous with broad, dark, sclerotic centers and narrow hyaline margins; leaves to 45(–55) cm long; petioles slightly shorter than to usually longer than laminae; petiolar scales usually decid-

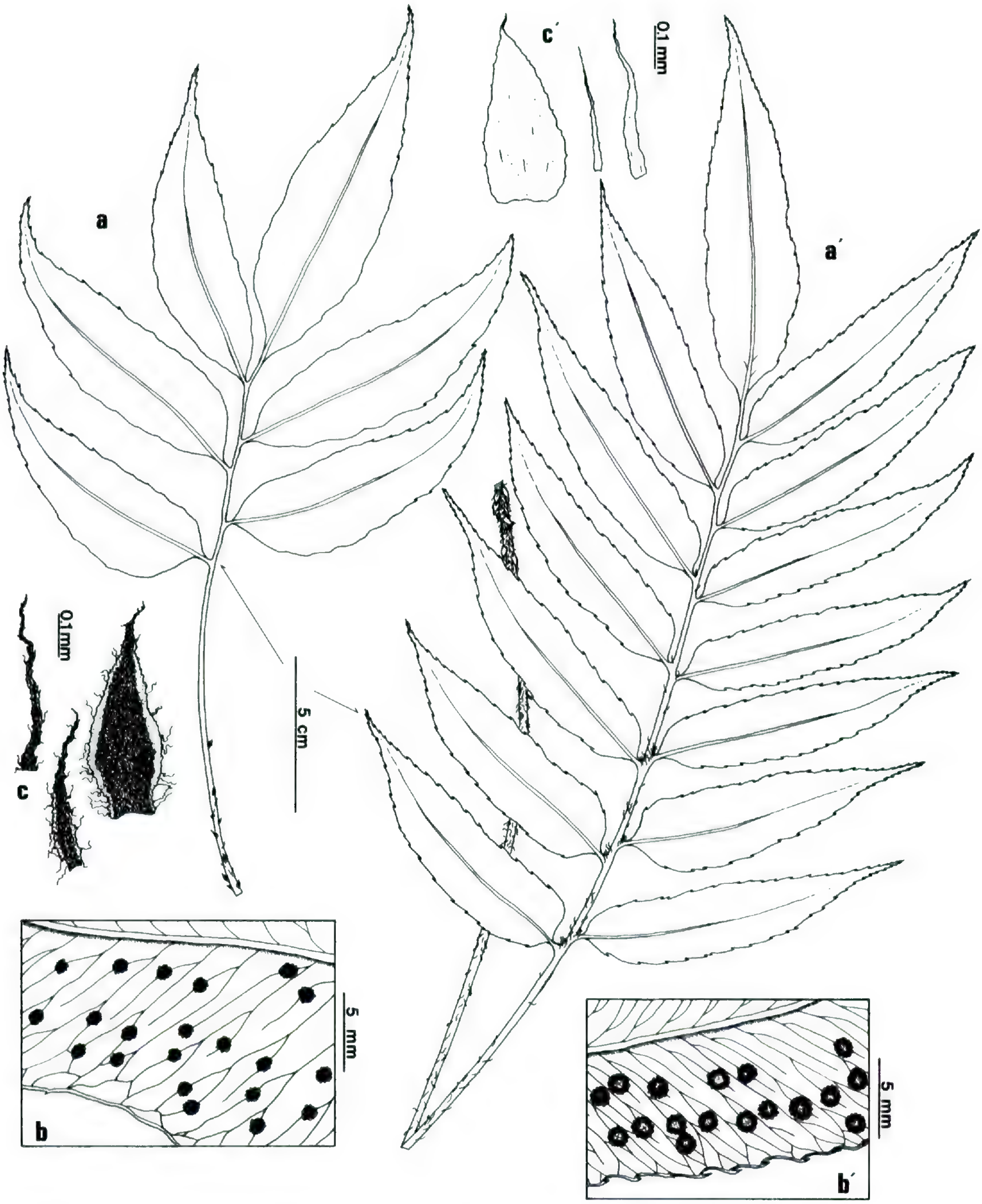


Figure 9. *Phanerophlebia gastonyi* (a–c) and *P. nobilis* var. *remotispora* (a′–c′). —a, a′. Representative leaves. —b, b′. Details of pinnae showing venation, sori, indusia, and pinna margins. —c, c′. Representative series of petiolar scales. (a–c from *Yatskievych et al. 85–182*; a′–c′ from *Yatskievych 85–186*.)

uous with age, mostly not overlapping, much like rhizome scales, the broadest 2 mm wide, the reduced hairlike structures uncommon among the broader scales; pinnae (0–)1–3(–4) pairs, to 12(–15.5) cm long, ovate to lance-ovate, sometimes somewhat falcate, the apex acute to attenuate, the base obliquely cuneate to rounded, sometimes nearly equilateral, the margins entire to slightly undulate proximally, spinulose-serrulate only in distal half; buds absent from axils of distal pinnae; veins with 1–3 series of regular marginal anastomoses, 2–4-branched; sori in (1–)2–4 series between costa

and margin; sori exindusiate; spores 30–42 μm long. Chromosome number: $n = 41$.

Illustrations. Figure 9a–c; see also Mickel and Beitel (1988: 520, as *P. juglandifolia*).

Phanerophlebia gastonyi grows in moist soil, less commonly on fissured limestone rock faces, in shaded understory of cloud forests and montane rainforests; 900–2200 m; southern Mexico (Chiapas, Oaxaca, Veracruz) (Fig. 10).

Specimens of *Phanerophlebia gastonyi* have been identified by previous workers as *P. juglandifolia*, but molecular studies (Yatskievych et al., 1988) have identified it as a progenitor of that species. The two taxa are very similar morphologically, but can be separated by the characters included in the key. Diploid *P. gastonyi* is treated here at species rank, rather than as a variety or subspecies of *P. juglandifolia*, because isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have suggested that the latter, tetraploid taxon is of allopolyploid origin, with the other diploid parent not yet identified.

Representative specimens. MEXICO. **Chiapas:** 13 km N of Berriózabal, *Breedlove & Smith 21652* (DS, F, MICH, NY). **Oaxaca:** trail from San Pedro Nolasco N to the Llano Verde, *Mickel & Hellwig 3786B* (NY). **Veracruz:** ca. 12 km S of Misantla, *Conant 726* (GH, MEXU).

3. Phanerophlebia haitiensis C. Christensen, Kongl. Svenska Vetenskapsakad. Handl. III 16: 42 + pl. 10, figs. 1–4. 1937. *Cyrtomium haitiense* (C. Chr.) C. V. Morton, Amer. Fern J. 47: 55. 1957. TYPE: Haiti. Massif de la Selle, Ganthier, Badeau, deep gulch above Badeau, alt. 2000 m, 28 Jan. 1925, *Ekman 3119* (holotype, S; isotypes, BM, US).

Plants not strongly scented; rhizomes to ca. 10 mm diam., apparently deeply seated in substrate, short-repent to ascending, not branched at maturity; rhizome scales 4.5–7.0 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, erose-denticulate, with few, short cilia at base, concolorous, brown (rarely lighter colored with age); leaves to 50 cm long; petioles slightly shorter than to longer than laminae; petiolar scales usually deciduous, loosely overlapping, much like rhizome scales, the broadest ca. 3 mm wide, grading into reduced, hairlike structures above; pinnae 1–4 pairs, to 9 cm long, lanceolate to lance-ovate, usually falcate, the apex acute to attenuate, the base unevenly cuneate and lacking an acroscopic auricle, the margins sometimes slightly undulate, spinulose-serrulate in distal half; buds absent from axils of distal pinnae; veins with irregular marginal anastomoses, 2–3-branched; sori in 1–2(–3) series between costa and margin; indusia 0.7–1.1 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 35–56 μm long, often lacking a well-developed perispore. Chromosome number unknown.

Illustrations. See original description.

Phanerophlebia haitiensis grows on protected limestone cliffs; 2000–2500 m; Central America (Guatemala, Honduras), Haiti (Fig. 10).

This perplexing taxon is apparently of hybrid origin, based on its irregularly sized spores with reduced perispore deposition and its irregularly anastomosing veins. Examination of stomates from a cleared pinna fragment indicates a size range in agreement with polyploid taxa in the genus (see previous discussion). It has not been re-collected in Haiti since Ekman's original specimens (both from the same locality). John T. Mickel (pers. comm.) has searched for this species and failed to locate it. It is therefore presumed extinct there.

Single collections from Guatemala and Honduras (see below and Fig. 10) share with the Haitian collections the irregularly anastomosing venation and spores of variable size with apparently reduced perispore deposition. The Guatemalan collection possesses few mature sporangia, however, and plants at this locality require further study. Smith (1981) suggested affinities between this species and *P. lindenii* E. Fourn., which is here treated as a synonym of *P. pumila* (M. Martens & Galeotti) Fée. See the treatment of the latter species for further discussion.

Specimens examined. HAITI. Massif de la Selle, Croix des Bouquets, ravine between M. Mérillon et M. Badeau, type locality, *Ekman 7793* (F, GH, MICH, NY, US). GUATEMALA. **Huehuetenango:** km 324–325 on Ruta Nacional 9N between Chemal and San Juan Ixcoy, Sierra de los Cuchumatanes, *Beaman 3056* (GH, TEX, UC). HONDURAS. **Santa Bárbara:** 7 km N of El Mochito on E slopes of Mt. Santa Bárbara, *Moran 5706* (MO).

4. Phanerophlebia juglandifolia (Humboldt & Bonpland ex Willdenow) J. Smith, J. Bot. (Hooker) 4: 187. 1841. *Polypodium juglandifolium* Humb. & Bonpl. ex Willd., Sp. Pl. (ed. 4) 5: 195. 1810. *Amblia juglandifolia* (Humb. & Bonpl. ex Willd.) C. Presl, Tent. Pterid. 185. 1836. *Aspidium juglandifolium* (Humb. & Bonpl. ex Willd.) Kunze ex Klotzsch, Linnaea 20: 363. 1847. *Cyrtomium juglandifolium* (Humb. & Bonpl. ex Willd.) T. Moore, Index Fil. lxxxiii. 1857. *Dryopteris juglandifolia* (Humb. & Bonpl. ex Willd.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. *Polystichum juglandifolium* (Humb. & Bonpl. ex Willd.) Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 191. 1899. TYPE: Venezuela. Monagas: Caripe, *Humboldt & Bonpland s.n.* (holotype, B—Herb. Willd. 19688, sheets 1a, 1b; isotypes, P, NY (fragment)).

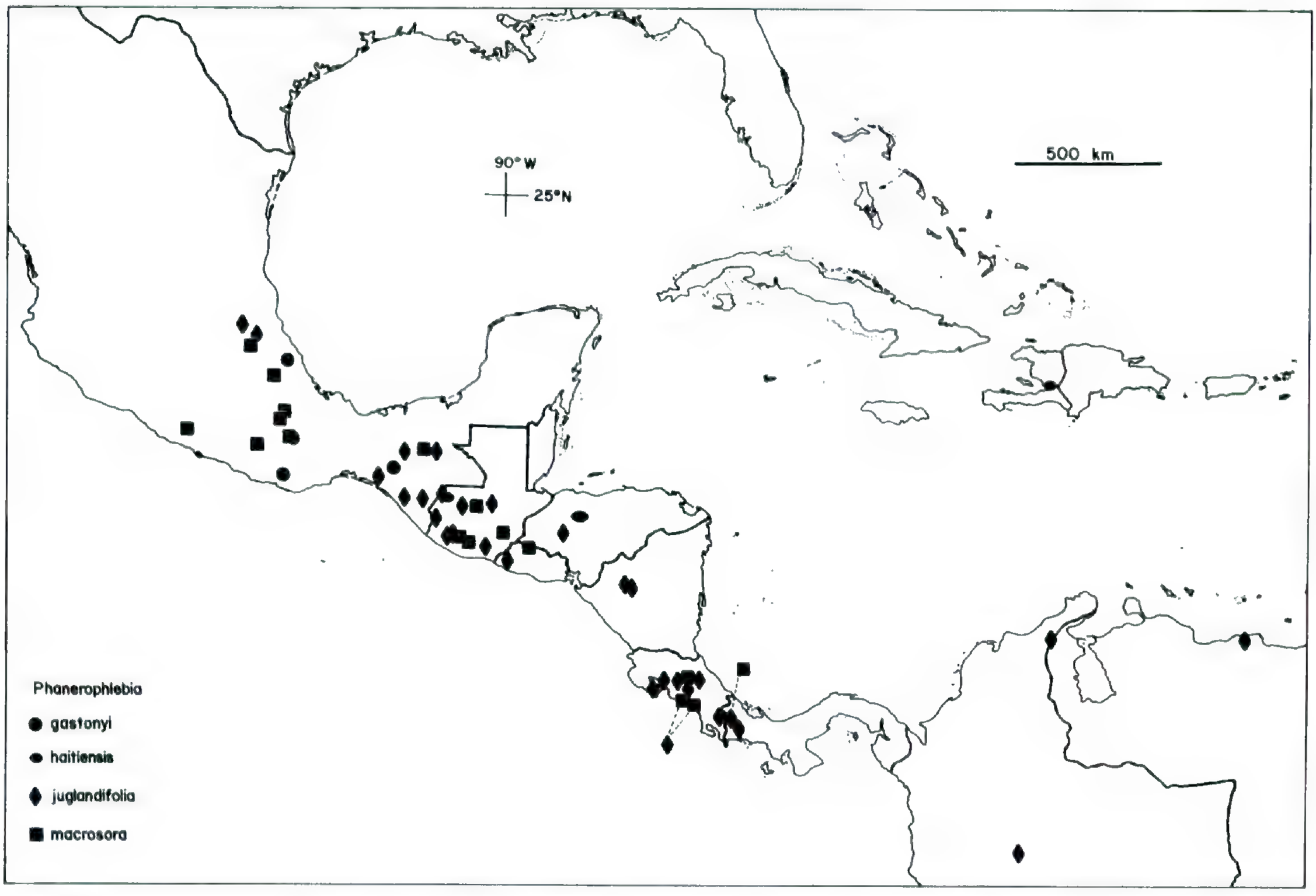


Figure 10. Distributions of *Phanerophlebia gastonyi*, *P. haitiensis*, *P. juglandifolia*, and *P. macrosora*, based upon herbarium specimens examined.

Plants not strongly scented; rhizomes to ca. 7 mm diam., generally deeply seated in substrate (sometimes superficial), short-repent to nearly erect, not branched at maturity; rhizome scales 6.0–10.5 mm long, 3–5 mm wide, lanceolate, ciliate, bicolorous with broad or sometimes narrow, dark brown, somewhat sclerotic centers and hyaline margins as wide as centers or narrower; leaves to 60(–85) cm long; petioles shorter than to slightly longer than laminae; petiolar scales subpersistent, overlapping and often dense, much like rhizome scales, the broadest 4 mm wide, grading into reduced, hairlike structures; pinnae 2–4(–6) pairs, to 17.5 cm long, ovate to lance-ovate, usually somewhat falcate, the apex attenuate, the base obliquely cuneate to rounded, the margins often slightly undulate proximally, spinulose-serrulate in distal half or more commonly in distal two-thirds; buds present on at least some leaves in each population, the gemmae in axils of distal pinnae (rarely in axils of more proximal pinnae); veins with 1–3 series of regular marginal anastomoses, 3–5-branched; sori in 2–4(–5) series between costa and margin; sori exindusiate; spores 41–60 μm long. Chromosome number: $n = 82$.

Illustrations. Humboldt et al. (1825, 7: pl. 665, as *Polypodium juglandifolium*), Underwood (1899: pl. 359–360, pinna), Vareschi (1969: 368, pinna); Stolze (1981: 166, as *Cyrtomium juglandifolium*).

Phanerophlebia juglandifolia grows in moist soil of ravines and slopes, associated with limestone or volcanic substrate, in rainforests and evergreen cloud forests, rarely in pine-oak forest; (350–)700–2700 m; eastern and southern Mexico (Chiapas and disjunctly in Hidalgo and Veracruz), nearly throughout Central America, to Colombia and Venezuela (Fig. 10).

Previous workers were unaware that *Phanerophlebia juglandifolia*, as traditionally circumscribed, was a heterogeneous mixture of a widespread, allotetraploid taxon (to which the type of this name can be ascribed) and one of its diploid progenitors, which is here treated as *P. gastonyi*. Unfortunately, the identity of the other parental taxon remains unclear. Compounding the problem of morphological circumscription of *P. juglandifolia* was the discovery of rare, naturally occurring hybrids between this species and *P. macrosora*. These hybrids, which are apparently restricted to the mountains of central Costa Rica, are sterile triploids of intermediate morphology, and were relatively commonly encountered in the single site where I was able to observe these plants. They are

morphologically variable, though most are robust plants with the overall aspect of *P. macrosora*. They can be separated from both parents by their somewhat smaller, bicolorous, petiolar and rhizome scales, irregularly anastomosing venation, highly reduced or absent indusia, and malformed spores (many of the sporangia also abort early in their development). The only specimens seen that represent this hybrid are both from medium elevations (1700–2000 m) in the volcanic mountains of central Costa Rica (Alajuela, La Ventolera, on S slope of Volcán de Poás, *Standley 34531* (GH, US); Heredia, 2 km SE of Sacramento on hwy. 114 from San José de la Montaña, S slope of Volcán Barva, *Yatskievych & McCrary 86–31a* (CR, IND, MO, NY)).

Representative specimens (of *P. juglandifolia*). MEXICO. **Chiapas:** above Finca Cuxtepec, mpo. Angel Albino Corzo, *Breedlove & Strother 46731* (CAS). **Hidalgo:** 8–9 km N de Ismolintla, mpo. Molango, *Hernández M., Cortés & Hernández M. 5916* (MEXU, MO). **Veracruz:** hacia el arroyo Toluca, desde la vereda que va a Tzimentey, mpo. Huayacocotla, *Palma G. 67* (XAL). GUATEMALA. **Alta Verapaz:** trail between Sepacuité and Secaquim, *Maxon & Hay 3289* (US). **El Quiché:** mountain slopes S of Nebaj, *Proctor 25075* (DS, LL, TEX, US). **Escuintla:** between Santa María de Jesus and Palín, *Standley 61300* (F). **Huehuetenango:** above San Juan Ixcoy, Sierra de Cuchumatanes, *Steyermark 50036* (F, US). **Quetzaltenango:** along road between La Finca Pirineos and Patzulín, *Standley 87078* (F, US). **San Marcos:** 1 mi. above Africa, ca. 3.3 mi. above Finca Armenia above San Rafael, *Croat 40940* (MO). EL SALVADOR. **Santa Ana:** NE slope of Cerro de los Naranjos, *Tucker 1288* (BH, GH, K, LL, MICH, NY, US). HONDURAS. **Lempira:** Celaque National Park, trail from Camp 1 to Río Naranjal, *Moran 5565* (MO). **Santa Barbara:** Cerro Santa Barbara, 10 km E de Lago Yojoga, *Clewell & Hazlett 3975* (MO). NICARAGUA. **Matagalpa:** Valle Palcila, *Moreno 7014* (MO). **Jinotega:** Cerro Ciale, SW of Jinotega, *Standley 10468* (F, US). COSTA RICA. **Alajuela:** Tapesco de Lacero, Alfaro Ruiz, *Smith 1463* (GH, NY). **Cartago:** Carpintera, *Brade & Brade 53* (GH). **Heredia:** Porrosatí de Barva, *Gómez 22207* (CR). **Puntarenas:** Monte Verde, around community along Río Guacimal below Lechería, *Hammel & Trainer 13825* (MO). **San José:** along Quebrada Tablazo and on forested slope above creek, NE part of Altos Tablazo, *Grayum & Schatz 5166* (MO). PANAMA. **Chiriquí:** 12 mi. from Gualaca on road to Cerro Hornito, *Antonio 1752* (MO). VENEZUELA. **Distrito Federal:** Cerro de Avila, Quebrada Chacaito, *Manara s.n.* (MO). COLOMBIA. **Cundinamarca:** Salto de Tequendam, Bogotá, *Voyage de J. Triana 61* (P). **Magdalena:** Sierra de Perijá, 10 km ENE of Manure, 3 km from Venezuelan border, *Grant 10799* (GH).

5. Phanerophlebia macrosora (Baker) Underwood, Bull. Torrey Bot. Club 26: 213. 1899. *Aspidium juglandifolium* (Humb. & Bonpl. ex Willd.) Kunze ex Klotzsch var. *macrosorum* Baker, J. Bot. 25: 25. 1887. *Cyrtomium macrosorum* (Baker) C. V. Morton, Amer. Fern J. 47: 55. 1957. TYPE: Costa Rica. Without further locality, 1886(?), *Cooper* s.n. (holotype, K; isotypes, GH, NY (fragment), US).

Phanerophlebia guatemalensis Underw., Bull. Torrey Bot. Club 26: 214. 1899. TYPE: Guatemala. Quiché: San Miguel Upsantán, alt. 7000 pp., Apr. 1892, *Heyde & Lux* s.n. [herb. J. Donnell-Smith 3241] (holotype, NY; isotypes, GH, P, US).

Plants with a strong, unpleasant, skunklike odor when fresh; rhizomes to ca. 20 mm diam., deeply seated in substrate, erect or ascending, unbranched at maturity; rhizome scales 10–15 mm long, 5–7 mm wide, ovate to lance-ovate, erose-ciliate, concolorous (rarely with a slightly darkened central area); leaves 0.7–2.7 m long; petioles shorter than to nearly as long as laminae; petiolar scales persistent, dense and overlapping, much like rhizome scales, the broadest ca. 7 mm wide, mixed with reduced, hairlike structures above; pinnae (4–)6–17 pairs, to 27 cm long, narrowly oblong-lanceolate, occasionally slightly falcate, the apex attenuate, the base obliquely cuneate to rounded and lacking an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 3–4-branched; sori in 2–4 series between costa and margin; indusia 0.6–1.1 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μm long. Chromosome number: $n = 41$.

Illustrations. Smith (1981: 330), Stolze (1981: 166, as *Cyrtomium macrosorum*), Mickel and Beitel (1988: 520).

Phanerophlebia macrosora grows in moist soil in mesic ravines and on shaded slopes, usually with igneous or volcanic substrate, in montane rainforests and cloud forests, rarely in oak forests; 1800–3200 m; eastern and southern Mexico (Chiapas, Hidalgo, Oaxaca, Veracruz), through Central America, to western Panama (Fig. 10).

This interesting species is easily recognized by its large, coarsely divided, brittle leaves with a thick, coriaceous texture, by its densely and persistently scaly petioles, and by its pronounced skunklike odor (first brought to my attention by John T. Mickel). This pungent, disagreeable odor is noticeable from more than 10 m in the field and can be an aid in locating plants. The compounds responsible disappear during drying and have not been identified, although some mixture of volatile terpenoids is suspected. The species is of further interest within the genus (and among ferns in general) for its geniculate petioles. The petiole bases deviate nearly horizontally from the deepset, nearly erect rhizomes, then curve upward, but the laminae are again oriented nearly horizontally. The leaves thus have a pronounced sigmoidal curvature at maturity.

For a discussion of the rare, sterile hybrid be-

tween this species and *Phanerophlebia juglandifolia*, see the treatment for that species, above.

Representative specimens. MEXICO. **Chiapas:** SW side of Cerro Mozotal, 11 km NW of junction of road to Motozintla along road to El Porvenir, *Breedlove 41713* (DS). **Guerrero:** El Asoleadero, 15 km W de Camotla, *Rzedowski 18531* (ENCB). **Hidalgo:** El Potrero, carretera Metepec-Tenango de Doria, *Gimate L. 975* (ENCB, F, MEXU, NY). **Oaxaca:** 26–29 km NE of Teotitlán del Camino, vicinty of pass at Pto. Soledad, *Mickel & Hellwig 4156* (NY). **Veracruz:** La Pandura, camino del Ingenio El Rosario a Xico, mpo. Xico, *Narave F. 319* (XAL). GUATEMALA. **Chimaltenango:** 8 km S of Acatenango, *Madison 670* (GH). **El Progreso:** between Finca Piamonte and top of Montaña Piamonte, along Joya Pacayal, *Steyermark 43709* (F, US). **Quetzaltenango:** slopes of Volcán de Zunil at and above Aguas Amargas, *Standley 65420* (F). **San Marcos:** slopes of Cerro Tumblador, ca. 15 km W of San Marcos, *Williams, Molina R. & Williams 23058*(US). **Solalá:** Volcán San Pedro, N-facing slopes toward Lago de Atitlán, above village of San Pedro, *Steyermark 47248* (UC). **Suchitepéquez:** Volcán Santa Clara, between Finca El Naranjo and upper slopes, *Steyermark 46717* (F, US). EL SALVADOR. **Chalatenango:** Cerro El Pital, *Seiler 418* (F). COSTA RICA. **Cartago:** road up Volcán Irazu, 0.5 mi. above Sanatorio Duran, ca. 9 mi. above Cartago, *Rossbach 3079* (GH). **Heredia:** N of Heredia, ca. 1 km beyond Porrosatí, *Lellinger & White 1679* (F, US). **Puntarenas:** upper Río Burú, *Gómez, Chacón, Chacón & Herrera 21432* (CR, MO). **San José:** Forêts du Copay, *Tonduz 11930* (US). PANAMA. **Chiriquí:** Volcán de Chiriquí, 7.3+ mi. from Boquete, *Armond 534* (CAS, F).

6. Phanerophlebia nobilis (Schlechtendal & Chamisso) C. Presl, Tent. Pterid. 85. 1836. *Aspidium nobile* Schltdl. & Cham., Linnaea 5: 610. 1830. *Cyrtomium nobile* (Schltdl. & Cham.) T. Moore, Index Fil. lxxxiii. 1857. TYPE: Mexico. Veracruz: Hacienda de Laguna, Oct. 1828, *Schiede* s.n. (holotype, HAL).

Plants not strongly scented; rhizomes to ca. 15 mm diam., erect or ascending, usually unbranched at maturity; rhizome scales 3.5–7.5 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, denticulate or deciduously ciliate, concolorous, brown; leaves to 1.2 m long; petioles shorter than the laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hairlike structures above; pinnae (2–)6–17 pairs, to 17 cm long, lanceolate to linear-lanceolate, usually at least somewhat falcate, the apex attenuate, the base obliquely cuneate, rarely subcordate and with an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free or with 1–3 series of areoles toward the margin (these sometimes distributed irregularly), 1–3-branched; sori in 2–4 series between costa and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μm long. Chromosome number: $n = 41$.

Two varieties are separable based on differences in venation. These were accorded specific rank by earlier workers, based on the view that reticulate versus free venation was a character of fundamental importance in the classification of *Phanerophlebia* species. The discovery that there are no other morphological characters that reliably separate these two taxa correlates with results from chloroplast DNA analyses, which also suggest a close affinity between the two (Yatskievych et al., 1988). *Phanerophlebia remotispora* has previously been classified closer to *P. juglandifolia* than to *P. nobilis*, based on the assumption that reticulate venation had arisen only once in the group. Studies contrasting *P. juglandifolia* and *P. remotispora* (Yatskievych, 1990; Yatskievych et al., 1988) showed that these two taxa are consistently and readily separable using morphological, isozymic, and chloroplast genomic characters. It is of interest that data from chloroplast DNA analyses also indicated that reticulate venation has arisen independently twice in the genus (Yatskievych et al., 1988).

The varietal designation is here used for two apparently interfertile morphotypes within a species, lacking sharp biogeographic discontinuities, and which are separated only by a single morphological character whose genetic basis remains unknown. The two varieties of *Phanerophlebia nobilis* are sympatric throughout much of Mexico, except for the absence of variety *remotispora* in the northwestern portion of the species' range, but the two varieties have not often been found growing together (see below).

6a. **Phanerophlebia nobilis** var. **nobilis**

Venation free, or with a few, rare anastomoses.

Illustrations. Kunze (1844: pl. 67, as *Aspidium nobile*), Mickel and Beitel (1988: 517).

Phanerophlebia nobilis var. *nobilis* grows in moist soil, rarely on rock faces (in sinks), with limestone, igneous and volcanic substrate; shady, mesic ravines in oak, pine-oak, pine, or pine-fir forests, rarely in cloud forests, often associated with *Alnus*, or other streamside trees; 1000–2800(–3200) m; Mexico (Chiapas, Chihuahua, Distrito Federal, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Tlaxcala, Veracruz), to be

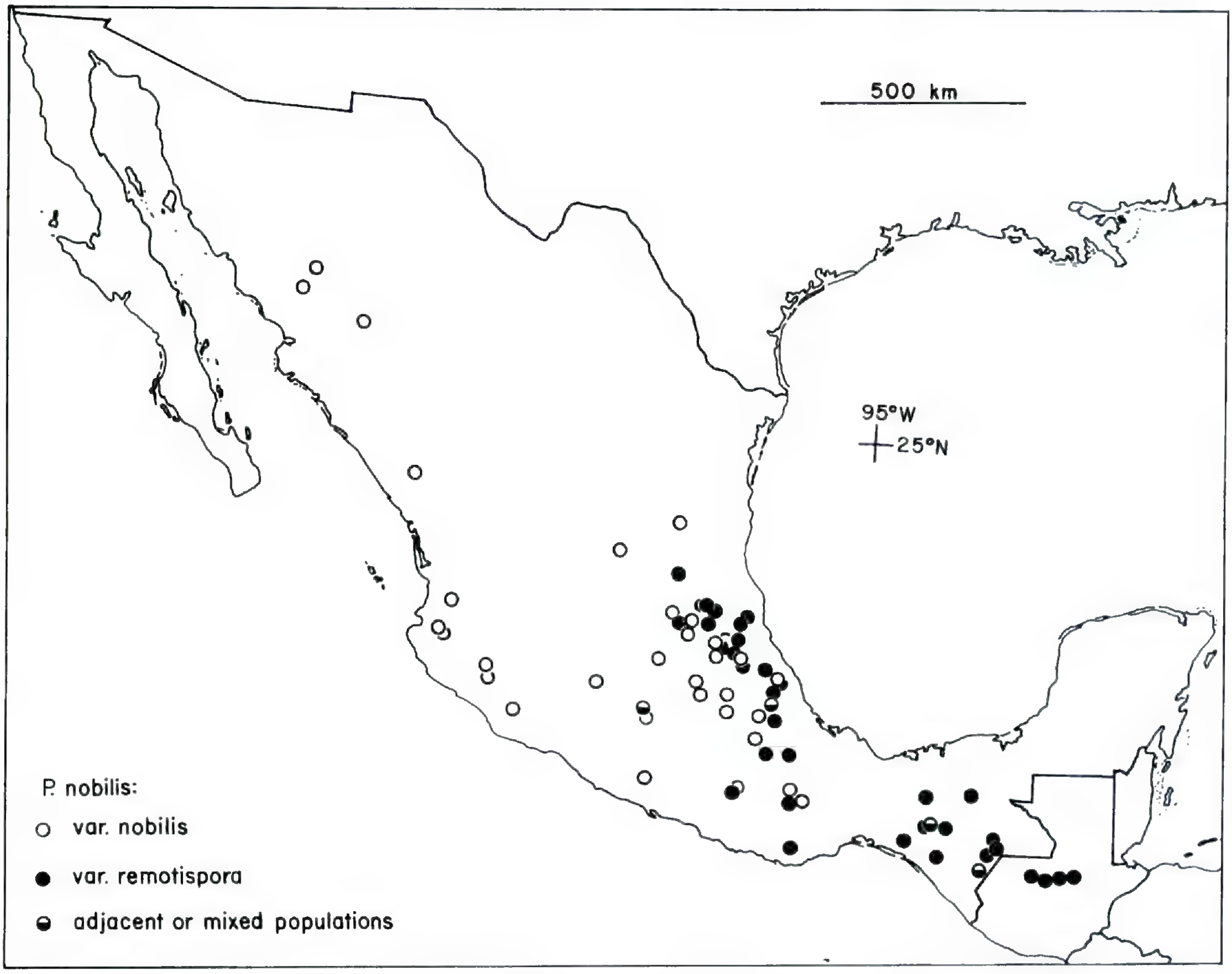


Figure 11. Distributions of *Phanerophlebia nobilis* var. *nobilis* and var. *remotispora*, based upon herbarium specimens examined.

expected in all states except the Yucatán peninsular lowlands and the Baja California Peninsula (Fig. 11).

The single collection known from Chiapas is morphologically atypical and was ascribed to *Phanerophlebia macrosora* by Smith (1981), who also noted its odd morphology. A single specimen labeled as having originated from Brazil (*Rio Grande do Sul*, Porto Alegre, Gebüsch unter der Rua da Independencia, *Reineck s.n.* (GH)) either represents an escape from cultivation or more probably a mislabeled specimen (Alan R. Smith, pers. comm.).

Plants of this variety tend to have somewhat shorter leaves (to 75 cm) than those of variety *remotispora* and commonly have fewer than 10 pairs of lateral pinnae. These differences disappear under common greenhouse culture, and are probably under environmental rather than genetic control. In central and southern Mexico, variety *nobilis* is often found at somewhat higher elevations and in coniferous forests, although there is nearly total congruence of elevational ranges between the two varieties.

Representative specimens. MEXICO. **Chiapas:** Mt. Male, near Porvenir, *Matuda 4688* (LL, MO, NY). **Chihuahua:** Sierra Charuco, Arroyo Hondo, *Gentry 7988* (ARIZ, DS, MEXU, MICH, US). **Distrito Federal:** Cañada de Contreras, cerca del Primer Dinamo, *Rzedowski 27212* (DS, ENCB, F, LL, MICH). **Guerrero:** 32–40 km by road W of Chilpancingo, near and above lumber town of Omiltemi, *Anderson & Laskowski 4363* (ENCB). **Hidalgo:** 4 km N de Tlahuelompa, mpo. Zacualtipán, *Riba 66* (MEXU). **Jalisco:** 1 km above settlement of El Isote, in pine-fir zone above Jazmín, NW slopes of Nevado de Colima, *McVaugh 10125* (MEXU, MICH, MO, US). **México:** 3 km E de San Rafael, mpo. Tlalmanalco, *Cruz C. 1649* (ENCB). **Michoacán:** Cuincho [Cointzio], près Morelia, *Arsène s.n.* (F, GH, P). **Morelos:** Cerro de El Tepozteco, mpo. Tepoztlán, *Camacho G. 10–58* (ENCB). **Oaxaca:** trail from San Pedro Nolasco N to the Llano Verde, *Mickel & Hellwig 3786a* (NY). **Puebla:** Puente del Emperador, *Lyonnet 3240* (MEXU, US). **Querétaro:** Agua Blanca, 10 km S de Pinal de amoles, *Fernández & Zamudio 992* (MO). **San Luis Potosí:** in montibus San Luis Potosí, *Schaffner s.n.* (NY). **Sinaloa**: 2.8 mi. NE of El Paraiso,

60 mi. SW of El Salto, road between Durango, Dgo. and Villa Union, Sin., *Ownbey & Ownbey 1936* (GH, US). **Sonora:** Curohui, Río Mayo, *Gentry 3660* (ARIZ, GH, MO, UC). **Tamaulipas:** above Casa Piedra on trail to Agua del Indio, region of sierra de Guatemala, ca. 7 km WNW of Gomez Farias, *Johnston 12777* (TEX). **Tlaxcala:** Tlaxcala, près Puebla, *Nicolas s.n.* (A, F, GH, K, MEXU, MICH, MO, P, UC, US). **Veracruz:** head of Orizaba Valley, *Copeland s.n.* (GH, MEXU, MICH, P, UC).

6b. Phanerophlebia nobilis var. **remotispora** (E. Fournier) Yatskievych, Novon 2: 446. 1992. *Phanerophlebia remotispora* E. Fourn., Mexic. Pl. 1: 100. 1872. *Cyrtomium remotisporum* (E. Fourn.) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Veracruz: Orizaba, Izhuatlancillo [Ixhuatlancillo], Aug. 1865–1866 [sheet at K = 20 May 1866], *Bourgeau 2349* (holotype, P; isotypes, BM, GH, K, MICH, MO, NY, P, US).

Venation commonly anastomosing toward the margins, with 1–3 series of areoles, these sometimes distributed irregularly. For further comparison with variety *nobilis* see treatment of that variety, above.

Illustrations. Figure 9a′–c′; see also Stolze (1981: 166, as *Cyrtomium remotisporum*), Mickel and Beitel (1988: 520, as *Phanerophlebia remotispora*).

Phanerophlebia nobilis var. *remotispora* grows in moist soil, rarely on rock faces (in sinks), with limestone, igneous and volcanic substrate, in mesic ravines and on slopes, in oak, pine-oak, and pine forests, cloud forests, less commonly in montane rainforests or deciduous or subdeciduous forest associations; also found along brushy roadsides, in overgrown coffee plantations, and in some disturbed or secondary forests; (300–)600–2300 m; southern and eastern Mexico (Chiapas, Hidalgo, México, Michoacán, Oaxaca, Puebla, San Luis Potosí, Veracruz), Guatemala (Fig. 11).

This is the only *Phanerophlebia* taxon to be found in secondary forests or disturbed roadside areas. The single collection from Michoacán is a mixed gathering with the sheet cited from CM representing variety *remotispora* and the other sheets (at A, GH, K, MEXU, MICH, MO, P, and UC) representing variety *nobilis*.

Representative specimens. MEXICO. **Chiapas:** slope of the sumidero in Tenejapa center, mpo. Tenejapa, *Breedlove 10768* (DS, MICH, US). **Hidalgo:** 5 km N de Tenango de Doria, hacia Huehuetla, *Hernández M. 3337* (ENCB, MO). **México:** Los Huevos, Distr. Temascaltepec, *Hinton 403* (NY). **Michoacán:** Cuincho [Cointzio], près Morelia, *Arsène 5415* (CM). **Oaxaca:** vicinity of lumber camp on top of Cerro San Felipe, on road off Axaca–Ixtlán Highway, 21 km N of Oaxaca, *Hellwig 361* (NY). **Puebla:** Villa Juarez, *Riba s.n.* (MEXU). **San Luis Potosí:** 3 km NE del Ejido de Xilitlilla, mpo. Xilitla, *Rzedowski 10571* (ENCB, NY). **Veracruz:** near Fortín above hydroelectric plant of Cervecería Moctezuma, *Croat 39411* (MO). GUATEMALA. **Alta Verapaz:** along road to El Ester (Lago Izabal), 2 mi. E of Highway 14 to Cobán, *Croat 41442* (CR, MO). **El Quiché:** falls of Río las Violetas, 2.5 mi. N of Nebaj, *Proctor 25446* (LL, US).

The two varieties of *Phanerophlebia nobilis* have only rarely been collected in mixed populations or at adjacent sites. Specimens of intermediate morphology are also occasionally encountered. These are characterized by pinnae with irregularly anastomosing venation, the areolae few and not distributed into a regular, marginal series. Such specimens appear to have well-formed spores. Intermediates between variety *nobilis* and variety *remotispora* include:

MEXICO. **Michoacán:** Cuincho [Cointzio], Río Grande, vic. of Morelia, *Arsène 5961* (GH, MO, US). **Veracruz:** Orizaba, *Fisher s.n.* (MO).

7. Phanerophlebia pumila (M. Martens & Galeotti) Fée, Mém. Foug. 5: 282. 1852. *Aspidium pumilum* M. Martens & Galeotti, Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 64 + pl. 17, fig. 1. 1842. *Cyrtomium pumilum* (M. Martens & Galeotti) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Oaxaca: Llano-Verde et del Carrizal, Mar. 1840, *Galeotti 6251* (holotype, BR, photos, BM, LL, MICH, UC; isotype, P).

Phanerophlebia lindenii E. Fourn., Mexic. Pl. 1: 100 + pl. 4. 1872. TYPE: Mexico. Chiapas: in pineto pr. Ciudad Real [San Cristóbal de Las Casas], Mar. [1838], *Linden* s.n. (holotype, P).

Plants not strongly scented; rhizomes to ca. 5 mm diam., usually superficial on substrate, erect or nearly so, not branched at maturity; rhizome scales 3–5 mm long, 2–3 mm wide, ovate to lance-ovate, ciliate-denticulate, concolorous, brown; leaves 4–30(–45) cm long (very short leaves sometimes fertile); petioles shorter than to longer than laminae; petiolar scales usually persistent, densely or loosely overlapping, filiform, the broadest 1.7 mm wide, grading into reduced hairlike structures; pinnae 0–3(–5) pairs, to 8(–12) cm long, ovate to lanceolate, usually somewhat falcate, the apex obtuse to attenuate, the base obliquely subcordate (occasionally cuneate) and sometimes with a small acroscopic auricle, the margins serrulate-denticulate nearly to base, rarely irregularly incised; buds absent from axils of distal pinnae; veins free or uncommonly with few marginal reticulations, 2–3-branched; sori

in 1–2(–3) series between costa and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled or subpersistent at maturity; spores 41–60 μm long. Chromosome number: $n = 82$.

Illustrations. Figure 12; see also original description, Underwood (1899: pl. 359–360, pinna), Stolze (1981: 166, as *Cyrtomium pumilum*), Mickel and Beitel (1988: 520).

Phanerophlebia pumila is epipetric on sheltered limestone rock faces, particularly those with overhangs, and in sinks; 2100–2950(–3700) m; southern and western Mexico (Chiapas, Guerrero, Michoacán, Oaxaca), Guatemala (Fig. 13).

Phanerophlebia pumila is a morphologically variable tetraploid of presumed allopolyploid origin. Unfortunately, although isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have suggested the presence of two parental genomes in this taxon, neither they nor data from chloroplast DNA variation in the genus (Yatskievych et al., 1988) have identified either of the two presumed progenitors involved. On the basis of habitat and morphology, *P. nobilis* may have been involved, but this taxon does not account for the reduced pinna number and leaf size, nor for the characteristic, narrow petiolar scales. One or both diploid progenitors of this species may be extinct, but should be sought by future collectors in the mountains of southern Mexico.

Although *Phanerophlebia pumila* has been characterized by some workers as having extremely reduced leaves with only 1–5 pinnae, the species is, in fact, extremely variable in this regard. Under greenhouse cultivation, plants with only 1–3 pinnae in the field often produced elongate leaves with up to 11 pinnae (also the largest number encountered in the field). Similar observations have been made independently by John T. Mickel (pers. comm.). Different leaves from various individuals of a single Mexican population (*Oaxaca,* Llano de Las Flores, near km post #130 on hwy. 175, N of Ixtlán de Juarez, *Yatskievych et al. 85–139* (CHAPA, IND, MEXU, MO, NY)) display great variation in pinna number, size, shape, and distribution (Fig. 12). Included within the range of variation demonstrated in Figure 12 are leaves referable to *P. lindenii* E. Fourn., a rare morphotype thought to differ from *P. pumila* in its cuneate (rather than subcordate) pinna bases. Larger leaves of *P. pumila* are extremely similar to smaller leaves sometimes displayed by plants of *P. nobilis* growing in ecologically suboptimal sites, such as the edges of sinkholes. Such plants can usually be determined correctly, based on differences in petiolar scales, but incomplete specimens cannot be determined without examination of stomatal sizes. A single mixed collection of these two species is known (MEXICO. **Michoacán:** Sierra Torrecillas, Distr. Coalcomán, *Hinton et al. 12428*; *P. pumila* = GH, K, LL, MEXU, MO, NY, US; *P. nobilis* var. *nobilis* = NY).

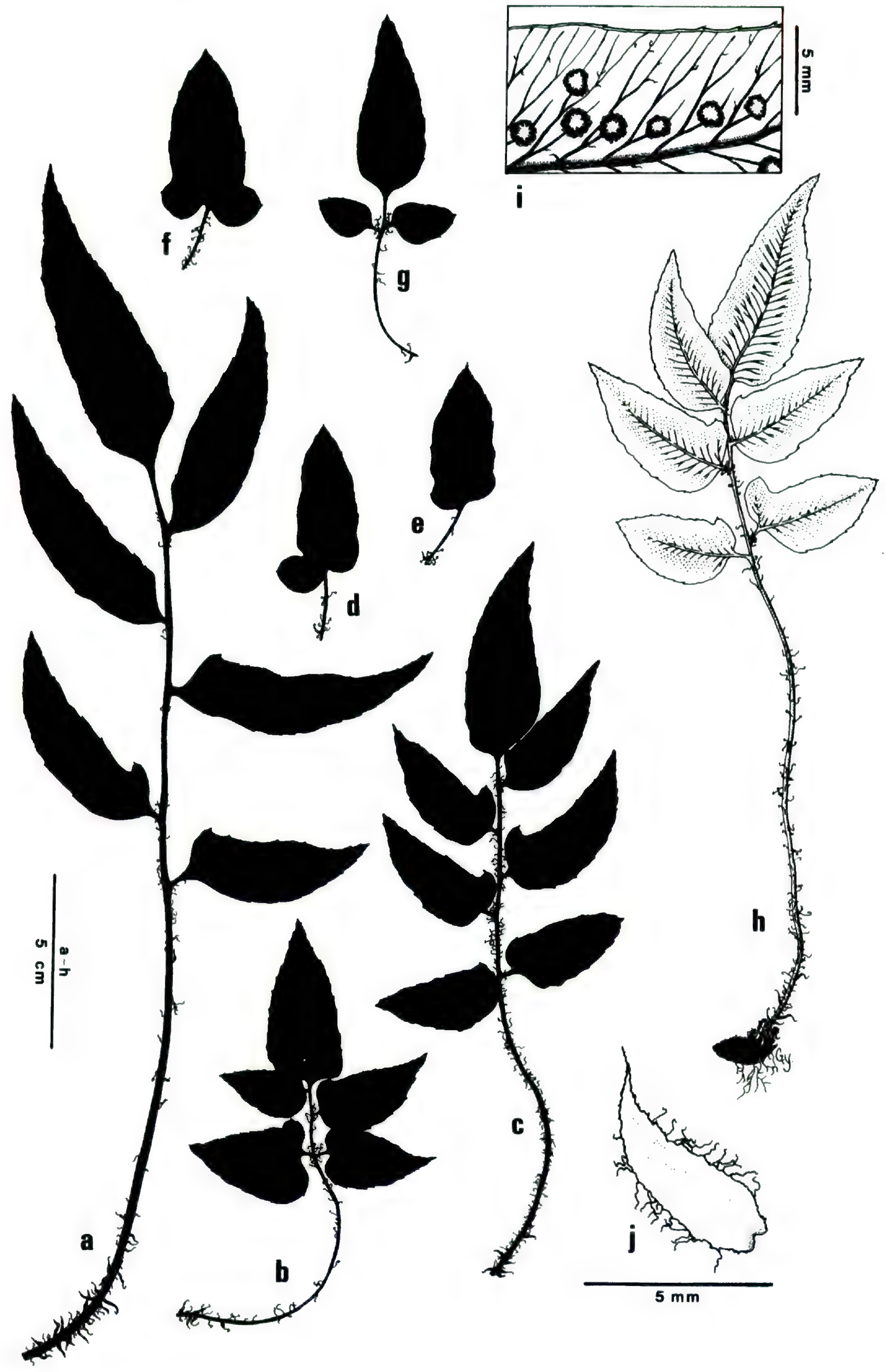
Representative specimens. MEXICO. **Chiapas:** 10 km E of El Porvenir along road from Huixtla to Siltepec, *Breedlove & Smith 31816* (DS, MICH, NY, TEX). **Guerrero:** top of the Sierra Madre near Chilpancingo, *Nelson 2222* (US). **Michoacán:** Sierra Torrecillas, Distr. Coalcomán, *Hinton 15935* (DS, ENCB, F, MEXU, NY, US). **Oaxaca:** trail N of San Pedro Nolasco to the Llano Verde, at the high point above the Llano Verde (Las Cruces), *Mickel 5377* (NY). GUATEMALA. **Huehuetenango:** between Tojquiá and Caxín, summit of Sierra los Cuchumatanes, *Steyermark 50211* (F, US).

8. Phanerophlebia umbonata Underwood, Bull. Torrey Bot. Club 26: 211. 1899. *Cyrtomium umbonatum* (Underw.) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Nuevo León: cool shaded cañons, Sierra Madre, near Monterrey, 14 June 1888, *Pringle 1982* (holotype, NY; isotypes, F, GH, MO, NY, P, UC, US).

Plants not strongly scented; rhizomes to ca. 15 mm diam., deeply seated in substrate, short-repent to ascending, often branched at maturity; rhizome scales 2.5–4.5 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, ciliate, concolorous, brown (rarely lighter colored with age); leaves to 90 cm long; petioles shorter than to nearly as long as laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hair-like structures above; pinnae 10–18 pairs, to 15 cm long, lanceolate to linear-lanceolate, usually falcate, the apex attenuate, the base cuneate to nearly truncate and lacking an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 1–3-branched; sori in 2–3 series between costa and margin, often submarginal; indusia 0.6–0.9 mm diam., firm, convex with a raised, darker umbo centrally, persistent and not shriveling at maturity; spores 41–60 μm long. Chromosome number: $n = 41$.

Illustrations. See original description; also Knobloch and Correll (1962: 164); Mickel (1979: 164).

Phanerophlebia umbonata grows in moist soil, less commonly among rocks, with igneous and limestone substrate, in sheltered canyons and ra-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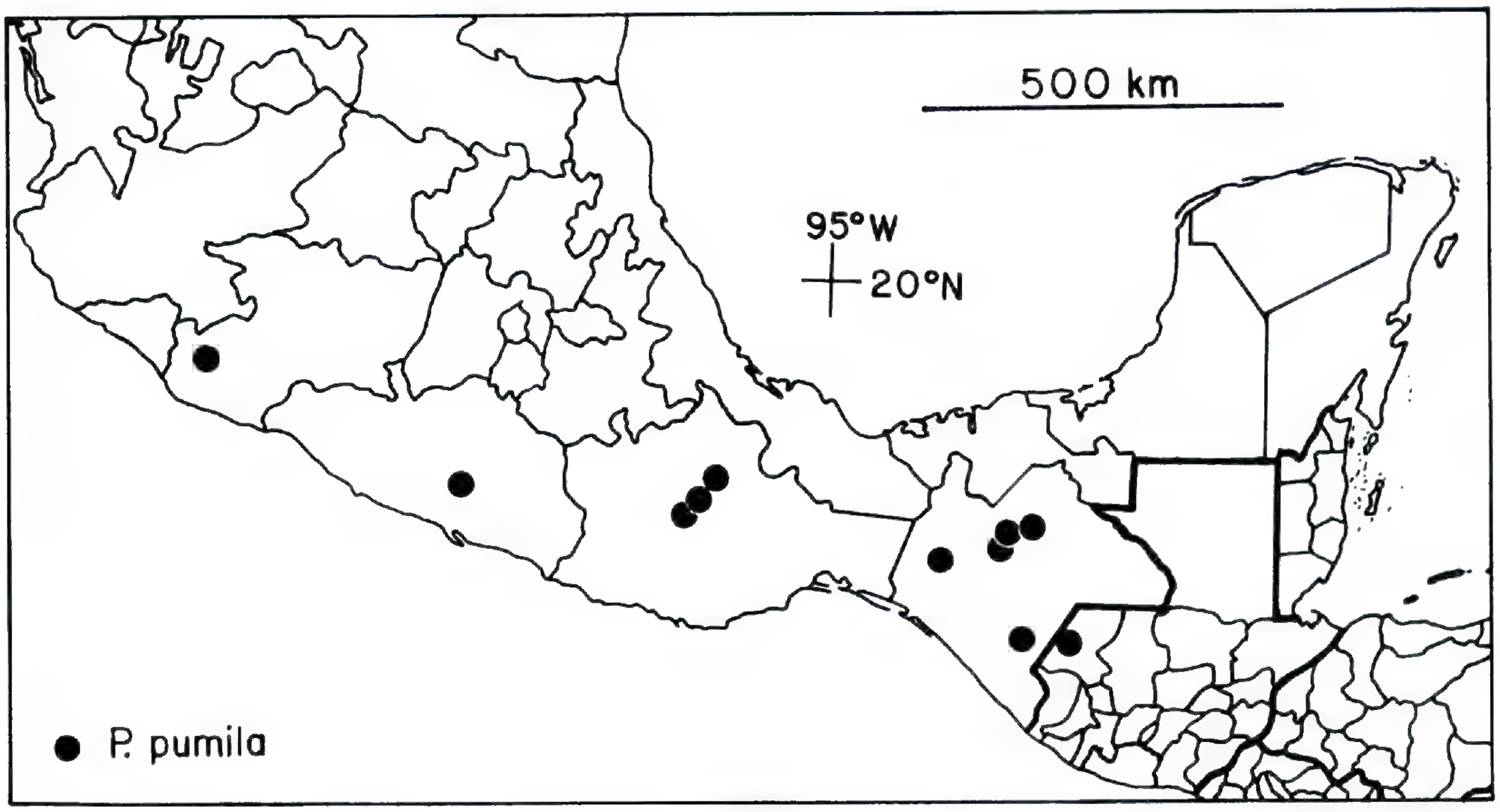

Figure 13. Distribution of *Phanerophlebia pumila*, based upon herbarium specimens examined.

vines, in oak and pine-oak forests, rarely in cloud forests; 550–1900 m; southwestern United States (Texas, known only from the Chisos Mountains in Brewster County), northern Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora, Tamaulipas) (Fig. 6).

Phanerophlebia umbonata is easily distinguished from related taxa by its persistent indusium with a raised, central umbo. Incomplete collections of sterile leaves of this species, however, are virtually impossible to distinguish from *P. nobilis* and can be difficult to distinguish from *P. auriculata*. The range of *P. umbonata* is generally to the northeast of that of *P. nobilis* and to the east of that of *P. auriculata*. The latter taxon can also usually be distinguished by its acroscopically auriculate pinnae, which possess a somewhat denser indument of reduced, uniseriate scales abaxially. The diploids *P. nobilis* and *P. umbonata* have been implicated in the parentage of tetraploid *P. auriculata*.

Representative specimens. U.S.A. **Texas:** Brewster County, damp places on side of Casa Grande, basin of the Chisos Mountains, *Warnock 178* (ARIZ, GH, TEX). MEXICO. **Chihuahua:** Guayanopa Canyon, Sierra Madre Mountains, *Jones s.n.* (CAS). **Coahuila:** Cañon de Milagro, E side of Sierra de los Guajes, ca. 12 km W of Hacienda de la Encantada, *Stewart 1532* (GH). **Nuevo León:** steep, rocky slope near Horsetail Falls, 6 km SW of Villa de Santiago, *Clausen 7555* (CU, GH, MEXU). **San Luis Potosí:** Route 90, 20.0 mi. E of Ciudad de Maiz, *Mickel 563* (ENCB, MICH). **Sonora:** Cañon de Tejas, Sierra Charuco, Sierra Madre Occidental, *Gentry 8119* (MICH, UC). **Tamaulipas:** km 17.6 (11 mi.) SW de Cd. Victoria, carretera 101, *Cowan 3728* (TEX).

Excluded Taxa

Phanerophlebia aurita Fée, Crypt. Vasc. Brésil 2: 70 + t. 100, fig. 1. 1873. = *Polystichum auritum* (Fée) Yatskievych.

Phanerophlebia caryotidea (Wallich ex Hook. & Grev.) Copel., Gen. Fil. 111. 1947. = *Cyrtomium caryotideum* (Wallich ex Hook. & Grev.) C. Presl.

Phanerophlebia caryotidea (Wallich ex Hook. & Grev.) Copel. var. *micropteris* C. Chr. ex Tard., Fl. Madagascar 1: 326. 1958. = *Cyrtomium micropteron* (Kunze) Ching.

Phanerophlebia falcata (L. f.) Copel., Gen. Fil. 111. 1947. = *Cyrtomium falcatum* (L. f.) C. Presl.

Phanerophlebia falcata (L. f.) Copel. var. *devexiscapulae* (Tag.) Ohwi, Fl. Jap. Pterid. 1957. = *Cyrtomium falcatum* (L. f.) C. Presl.

Phanerophlebia fortunei (J. Smith) Copel., Gen. Fil. 111. 1947. = *Cyrtomium fortunei* J. Smith.

Phanerophlebia fortunei (J. Smith) Copel. var. *cliv-*

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Figure 12. *Phanerophlebia pumila.* —a–g. Silhouettes of sample leaves from different plants in a single collection. —h. Habit. —i. Detail of pinna. —j. Rhizome scale. (a–j all from *Yatskievych et al. 85–139.*)

icola (Makino) Ohwi, Fl. Jap. Pterid. 69. 1957. = *Cyrtomium fortunei* J. Smith.

Phanerophlebia fortunei (J. Smith) Copel. var. *intermedia* (Tag.) Ohwi, Fl. Jap. Pterid. 69. 1957. = *Cyrtomium fortunei* J. Smith.

Phanerophlebia fraxinella (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtogonellum fraxinellum* (H. Christ) Ching.

Phanerophlebia hookeriana (C. Presl) Copel., Gen. Fil. 111. 1947. = *Cyrtomium hookerianum* (C. Presl) C. Chr.

Phanerophlebia macrophylla (Makino) Okuy. ex Ohwi, Fl. Jap. Pterid. 70. 1957. = *Cyrtomium macrophyllum* (Makino) Tag.

Phanerophlebia macrophylla (Makino) Okuy. ex Ohwi var. *tukusicola* Okuy., Coll. Ill. Wild Pl. Jap. 7: 41 + pl. 373, fig. 2. 1960. = *Cyrtomium macrophyllum* (Makino) Tag. var. *tukusicola* (Tag.) Tag.

Phanerophlebia nephrolepioides (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtomium nephrolepioides* (H. Christ) Copel.

Phanerophlebia semicordata (Sw.) Conz., Fl. Taxon. Mex. 1: 13. 1939. = *Cyclopeltis semicordata* (Sw.) J. Smith.

Phanerophlebia tachiroana Copel., Gen. Fil., 111. 1947. = *Cyrtomium hookerianum* (C. Presl) C. Chr.

Phanerophlebia vittata (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtomium lonchitoides* H. Christ [note that Copeland's use of the name *P. vittata* probably applied to *C. balansae* (Christ) C. Chr., but the type of the basionym *C. vittatum* H. Christ actually = *C. lonchitoides* (Ching, 1936)].

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Appendix 1. Exsiccatae.

A. Taxa of *Phanerophlebia* accepted
(1) *Phanerophlebia auriculata* Underwood
(2) *P. gastonyi* Yatskievych
(3) *P. haitiensis* C. Christensen
(4) *P. juglandifolia* (Humboldt & Bonpland ex Willdenow) J. Smith
(5) *P. macrosora* (Baker) Underwood
(6) *P. nobilis* (Schlechtendal & Chamisso) C. Presl
(6a) var. *nobilis*
(6b) var. *remotispora* (E. Fournier) Yatskievych
(7) *P. pumila* (M. Martens & Galeotti) Fée
(8) *P. umbonata* Underwood

B. Collections by collector and number (or collection date where no number was indicated).

Anonymous (det. G. Kunze) (6a); (herb. Jeanpert) without date or number (6b); 000806 (6a); on 26 Apr. 1917 (6b); on 7 Feb. 1919 (1).

Abbon G. [= Arsène 6287] (8); [= Arsène 6291] (8). Acosta & Dorantes 281 (6b). Aguirre C. on 4 Oct. 1975 (8). Alfaro in Feb. 1902 [herb. J. Donnell-Smith 8074] (4); 103 [herb. J. Donnell-Smith 8074] (4). Allart 48 (4). Anderson & Laskowski 4363 (6a). Antonio 1752 (4); 2861 (4). Armond 534 (5). Arreguín 435 (6a). Arsène on 6 July 1911 (6a); on 7 July 1911 (8); 1687 (6a); 5415 (6a, b mixed collection); 5961 (6a, b intermediate). Avendaño R. 00063 (6b).

Ballesteros & Ballesteros 371 (6a), 403 (6a). Barkley 14579A (8). Barkley, Webster (G.) & Rowell 7130 (8). Barrington 1211 (5). Bartlett 10095 (8); 10391 (8); 10406 (8); 10931 (8). Batalla & Bravo on 11 Mar. 1933 (6a). Beaman 3056 (3-vel. aff.). Benson 10947 (1). Berkman & Lee 65 (1). Boege 2737 (6a). Bonilla B. F-4322 (6b). Bonpland without date or locality (4). Botteri 63 (6b). Bourgeau on 20 May 1866 (6b); 45 (6b); 916 (6a); 917 (6a); 104 (6a); 1648 (6b); 2276 (6b); 2341 (6b); 2348 (6b); 2349 (6b). Boutin & Kimnach 3101 (6a). Boza without date or number (4). Brade (A.) 182 (4). Brade (A.) & Brade (C.) on 17 Dec. 1909 [herb. E. Rosenstock 161] (4); 9573 (4) . Breckon & Christman 622 (7). Breedlove 7368 (6b) 10768 (6b); 15242 (5); 15299 (5); 24996 (4); 25355 (6b); 25759 (6b); 26262 (5); 26778 (4); 26840 (4); 27697 (6b); 32942 (4); 33657 (6b); 34400 (4); 34615 (6b); 34692 (4); 34698A (4); 38770 (6b); 41708 (4); 41713 (5); 42564 (4);

48670 (4); 53211 (6b). Breedlove & Almeda 56931 (6b). Breedlove & Bartholomew 55521 (7). Breedlove & Dressler 29667 (6b). Breedlove & Smith (Alan) 21652 (2); 21748 (6b); 22330 (6b); 31320 (6b); 31433 (6b); 31495 (2); 31816 (7); 31881 (5); 32310 (6b); 32744 (6b). Breedlove & Strother 46731 (4). Breedlove & Thorne 21363 (6b); 30867 (2). Brenes in 1912 (4). Butterwick 53 (6a). Butterwick & Osborn 2530 (1). Bye 6989 (1); 7094 (6a); 7363 (6a).

Caballero 162 (4). Camacho G. 10–58 (6a). Camp 2561 (1); 2744 (6a). Carrillo 3 (6a). Castillo C. & Vázquez 1360 (6b); 1383 (6b); 1567 (6b). Castillo C., Nee & Benavides 2417 (6b); 2549 (6b). Chacón (I.), Herrera & Gómez (H.) 1765 (4); 1789 (4). Chase 7312 (6a). Chavarría & Lara 27 (4). Cházaro B. & Castillo Ch. 6789 (5). Chrysler 5575 (4). Chrysler & Roever 5611 (4). Cisneros 1649 (6a). Clausen 7555 (8); 7570 (8). Clewell & Hazlett 3975 (4). Cochrane 8449 (8). Conant 726 (2). Conant, Dorante, Kress & Barrington 727 (6b). Contreras 4956 (6b). Conzatti (C.) 2133 (5). Conzatti (C.), Conzatti (H.) & Gómez (T.) 2363 (5). Conzatti (C.) & Gómez (T.) 3482 (5). Conzatti (C.) & González 1138 (6b). Cooper in 1886(?) (5). Copeland on 13 Jan. 1938 (6a); on 18 Jan. 1938 (6b); on 8 Feb. 1938 (6b); on 21 Mar. 1938 (6b). Cornman 847 (4); 899 (4). Correll 13787 (1); 13788 (1). Correll & Gentry 23043 (1); 23241 (1). Correll & Johnston (I.) 21772 (1). Cory 26488 (8). Cosson 474 (6a). Cota & Gimate 7778 (6b). Cowan 3728 (8). Cowan & Valdés 3586 (8). Croat 39411 (6b); 39484 (6b); 39489 (6b); 39546 (6b); 40940 (4); 41442 (6b); 41474 (6b); 44033 (6b); Croat 46105 (6b); 47628 (4); 48839 (4); 67734 (4). Croat & Hannon 65955 (6b). Cruz C. 1649 (6a).

Darling on 6 Nov. 1961 (1). Darrow & Haskell 2059 (1). Darrow, Gould, Pultz & Phillips (W.) 2556 (1). Davenport without date or number (6a). Davidse 24437 (4). Davis on 7 Apr. 1946 (8). Deaver 4788 (1). del Campo on 11 Mar. 1933 (6a); on 20 May 1933 (6a). Dorfler 190 (4). Dressler 1613 (4); 1947 (8). Drushel 9538 (8); 9539 (8). Dunn (David) & Dunn (Don) 19082 (6b).

Edwards 364 (8). Ehrenberg 868 (6a). Ekman 3119 (3); 7793 (3).

Fendler 233 (4). Ferguson on 23 May 1988 (1). Fernández & Zamudio 992 (6a). Ferris in 1902 (1); 264–08 (1); 294 (1). Fink 62 (6b); Fink 66 (6b). Fisher on 9 Aug. 1924 (6a, b intermediate); on 14 Aug. 1926 (6b); 35365 (6b). Fournier 64 (6b). Fryxell & Anderson 3588 (6b). Funck 211 (4).

Galeotti 6251 (7); 6343 (6a). Gallegos H. 370 (6a). Gentry 3660 (6a); 7988 (6a); 8119 (8). Gereau & Martin 2011 (7). Ghiesbreght without date or number (7); 209 (7); 414 (4). Gilbert 34 (8). Gimate L. 975 (5). Gómez (L.) 360 (5); 528 (4); 3441 (5); 22207 (4). Gómez (L.), Chacón (I.), Chacón (R.) & Herrera 21424 (4); 21432 (5); 21489 (5); 21966 (4). Gómez H. on 3 Oct. 1982 (6a). Gómez-Pompa & Riba 381 (6b). González Q. 1641 (6b); 2419 (6a). Goodding 392–45 (1); 162–50 (1); 138–52 (1); 57–53 (1); 95–61 (1); 3070 (1); 6144 (1); 6145 (1); 6146 (1). Goodding & Hinckley F-3–39 (1); F-9–39 (1). Gould 4347 (1). Gould, Darrow & Haskell 2788 (1). Grant 10799 (4). Grayum, Poveda & Gómez-Laurito 8233 (5). Grayum & Schatz 5166 (4). Guillemin without date or number (6b); in 1866 (6a).

Hahn 172 (6a). Hallberg 848 (7); 1391 (6b); 1456 (6b). Hamilton, Stockwell & Aiello 982 (4). Hammel & Trainer 13825 (4). Hartman 578 (1). Harvey 996 (8). Hellwig 361 (6b); 442.5 (7). Hernández M. 3337 (6b). Hernández M. (R.), Cortés & Hernández M. (I.) 5916 (4). Hernández M. & Hernández V. 4251 (5). Herrera 3611 (5). Heyde & Lux in Apr. 1892 [herb. J. Donnell-Smith 3259] (6b); 3241 (5). Hinton 403 (6b); 1335 (6a); 3544 (6a); 12428 (6a–7 mixed collection); 15935 (7); 16913 (8); 17511 (8); 17707 (8). House & Andino 961 (4). Hunnewell on 20 Jan. 1941 (5); 14599 (5); 14600 (5).

Jiménez 78–21 (6a). Johnson 699 (6b). Johnston (I.) & Müller (C.) 1362 (8). Johnston (M.) 12777 (6a); 12782 (6a). Johnston (M.), Wendt & Chiang C. 10728 (1). Jones on 23 Sep. 1903 [loc. a] (1); on 23 Sep. 1903[loc. b] (8). Joyal 1911 (6a).

Karwinski in 1827 (6a). Kearney & Peebles 14485 (1). Kellerman 5774 (5). Kemp in Jan. 1902 (8). Kenoyer in Nov. 1937 (6a); in Dec. 1937 (8); 157 (8); 715 (6a). Kenoyer & Crum 3743 (8). Kerber on 26 Sep. 1882 (6b). Killip 5468 (5); 5488 (4). Knapp 1462 (4). Knobloch 1967 (8); 7011 (1). Koch 7670 (6a). Kruckeberg 4836 (8).

Lacás 154 (8); 247 (8); 371 (8); 486 (8). Lara & Chavarria 28 (4). Laughlin 96 (6b); 549 (6b). Leavenworth 93 (8); 801 (8). Leding 592 (1). Lee, Berkman & Tharp 46193 (1). Leland on 26 Sep. 1896 (8). Lellinger & White 1679 (5). Lemmon in Aug. 1882 (1); on 8 Aug. 1882 (1); on 12 Aug. 1882 (1); in Sep. 1882 (1); 321 (6b). León 17 (4). Leonard & Mickel 4122 (6a). Liebmann in Aug. (6b). Linden in 1838 (7); in Feb.(?) 1838 (7); 1551 (7); 1552 (7). Lint (M.), Lint (H.) & Haskell 1005 (1). Little & Sharp 9922 (7). Loomis & Peebles 5413 (1). Lorence & Cedillo T. 4212 (6a). Lorence, Martin & Cedillo T. 3268 (6a). Lyonnet 87 (6a); 765 (6a); 1481 (6a); 1533 (6a); 1633 (6a); 1926 (6a); 3240 (6a).

Madison 670 (5). Manara on 27 June 1976 (4). Marsh 236 (8); 268 (8); 1871 (8). Martin, Moore & Titley s.n. (6a). Matuda 193 (6b); 1324 (6b); 1365 (6a); 1893 (5); 4068 (5); 4688 (6a); 5230 (5); 18710 (6a); 18783 (6a); 26457 (6a); 28263 (6a); 28304 (6a); 30948 (6a). Maury 6752 (6b). Maxon 4935 (4); 5273 (5). Maxon & Hay 3289 (4). McAlpin 2021 (6b); 2024 (6a). McVaugh 10125 (6a); 11756 (6a); 14238 (6a); 20437 (6a); 22314 (5); 23304 (6a). Mears 231A (6a); 232 (6a). Mexia 1558 (6a). Meyer & Rogers 2581 (8); 2935 (8). Mickel 563 (8); 5377 (7); 6044 (2); 6182 (2); 7248 (6b). Mickel & Hellwig 3786A (5); 3786a (6a); 3786B (2); 4156 (5). Mickel & Leonard 5284 (5); 5384 (7); 5384A (7); 5384B (7). Mickel & Pardue 7047 (6a). Mohr 184 (6b). Montgomery & Root 7339C (8). Moore & Wood 4427 (6a). Morales 1953 (5). Moran 3035 (4); 4167 (4); 5565 (4); 5667 (4); 5706 (3). Morelos O. 5 (6a). Moreno 7014 (4). Moritz 10955 (4). Moya R. 34 (8). Müller (C.) 729 (6b); 2747 (8). Müller (C.) & Müller (M.) 353 (8). Münch in 1901 (6b); in Oct. 1901A (7); in Oct. 1901B (7); 61 (5); 74 (7).

Narave F. 319 (5); 370 (5). Nava & Cruz P. 14 (6a). Nee & Taylor 26813 (6b). Nelson (A.) & Nelson (R.) 1206 (1). Nelson (E.) 2222 (7). Nevling & Gómez-Pompa 2308 (6b). Nicolas on 4 Dec. 1910 (6a). Niles 447 (1).

Ojeda A. 19 (6a). Orzel 79–21 (8). Ownbey (G.) & Ownbey (F.) 1936 (6a).

Palacios-Rios 2901 (2). Palma G. 67 (4). Palmer 450 (1). Parry, Bigelow, Wright (C.) & Schott on 5 Mar. (1). Pennell 16852 (8). Perkins & Hall 3256 (8); 3294 (8). Peterson J-1751 (6a). Phillips (E.) 546 (1); 725 (1). Phillips (W.) & Reynolds 2946 (1). Pineda R. 607 (6a). Pittier 207 (4); 2982 (4). Pringle on 21 July 1884 (1); 3 (1); 831 (1); 1982 (8); 3403 (8); 5585 (6b); 13739 (8). Proctor 25075 (4); 25446 (6b). Puig 4105 (8); 4918 (6b). Purpus in June 1931 (6b); 1595 (6a); 2454 (6a); 2933 (6b); 2993′ (6b); 6427 (6b); 15414 (6b); 16024 (6b); 16476 (6b); 16578 (6b).

Rascon without date or number (6b). Rebolledo V. 291 (5). Reeves (B.) et al. 88–1 (1). Reeves (T.) R1202 (1). Reichenbacher 1135 (1). Reichenbacher & Van Devender (T.) 759 (1). Reineck in July 1899 (6a); in Sep. 1899 (6a); on 14 Sep. 1899 (6a). Rhoads in Mar. 1899 (6b). Riba without date or number (6b); 66 (6a); 1002 (6a). Riba, Tryon (R.) & Tryon (A.) 361 (6b). Riskind 1592 (1). Rivera 377 (5). Robinson without date or number (7). Rocha 00071 (8). Rollins & Tryon (R.) 5862 (8). Rossbach 3079 (5). Rowell & Barkley 16M595 (8). Roybal 583 (8); 617 (8). Ruiz O. in Aug. 1947 (6a). Runyon 720 (8); 975 (8); 985 (8). Rzedowski 679 (6b); 10056 (6b); 10571 (6b); 18531 (5); 19864 (6a); 26425 (6a); 27212 (6a); 27229 (6a); 34234 (6a).

Saborio 36 (4). Salinas, Rowell & Barkley 16M575 (8). Salvin 113 (4); without date or number (4, 5 mixed collection). Sánchez (J.) 32 (6a). Sánchez M. 164 (6a). Sánchez S. 445 (6b). Scamman 7087 (5). Schaffner in 1850–1855 (6b); in Aug. 1875 (6a); in 1876 (6a); 67 (6a); 82 (6a); 277 (6a); 461 (6b). Schiede in Oct. 1828 (6a). Seaton 49 (6b). Seibert 187 (4). Seigler (D.), Bohnstedt & Seigler (E.) DS-2550 (8). Seiler 418 (5). Sessé, Mociño & Maldonado 3853 (6a). Shreve 5434 (1). Skutch 742 (5). Smith (Alan) 510 (6a); 515 (6a). Smith (Austin) F24 (4); 48/134 (4); 1463 (4). Smith (C.) on 24 Dec. 1894 (6b); 2187 (6b); 2202 (6b). Smith (R.) M329 (8). Soxman (G.) & Soxman (F.) 362 (1). Spence 27 (6b). Sperling 4958 (2); 4994 (2). Sperry 178 (8). Standley 10468 (4); 32649 (4); 34531 (4 × 5 hybrid); 57840 (5); 60049 (5); 61300 (4); 65420 (5); 67247 (4); 84842 (4); 86672 (4); 87087 (4); 90066 (6b). Stanford, Lauber & Taylor 2085 (8). Stanford, Retherford & Northcraft 1069 (8). Stewart 523 (8); 1532 (8); 1533 (8); 2198 (1). Steyermark 36243 (5); 36871 (4); 37160 (4); 43709 (5); 46717 (5); 47248 (5); 50036 (4); 50211 (7); 55130 (4). Stork 1411 (4); 1558 (4); 1732 (4); 3143 (4). Studhalter 308 (1).

Taylor 364 (8). Tenorio L., Ramamoorthy & Lafrankie 3655 (6b). Tharp on 4 Sep. 1915 (8); 1817 (8). Thornber, Goodding & Nelson (A.) on 16 Mar. 1935 (1). Thorne & Lathrop 41308 (6b); 41784 (6b). Ton 1990 (5); 4840 (6b); 5320 (6b); 5686 (6b); 5889 (6b). Tonduz 11930 (5). Torres C. (R.), Torres C. (L.) & Martínez 7168 (6b). Torres R. 109 (4). Triana 61 (4). Tucker 1288 (4).

van der Werff & Herrera 7111 (4). Van Devender (T.) on 6 Feb. 1978 (1); on 13 Feb. 1977 (1); on 16 Aug. 1978 (8). Van Devender (T.) & McCarten on 24 Sep. 1977 (1). Van Devender (T.) & Van Devender (M.) on 28 Mar. 1976 (1). Vázquez T. 00345 (6b). Ventura A. 476 (6b); 623 (6b); 2660 (6a); 2694 (6a); 7967 (6b); 9265 (2); 12342 (6b); 13927 (6b); 15836 (6b); 16261 (6b). Verlet in Aug. 1851 (8). Virlet 28 (6a). von Rozynski 415 (8); 646 (8). von Türchheim in Feb. 1856 (6b); in Sep. 1885 [herb. J. Donnell-Smith 768] (6b); in Sep. 1886 [herb. J. Donnell-Smith 1051] (4); in 1907 (6b). Vovides, Rees & Vázquez (T.) 685 (6b).

Warnock 178 (8); 21779 (1). Waterfall 6635 (1). Waters 737 (1). Weber 6046 (5). Webster (G.) & Preston 2878 (8). Webster, (M.) 177 (8). Wendt, Lott & Olmstead 1946 (1). Wercklé 15 (5). White & Chatters 27 (8); 229 (8). Whitehouse on 11 Nov. 1931 (1); on 12 Sep. 1934 (1). Whitlach 16 (8). Whitson 598 (8). Wiggins 7139 (1); 13340 (6b). Williams (L.), Molina R. & Williams (T.) 23058 (5); 23862 (4). Windham 0059B (1); 0109B (1). Wooton on 14 May 1899 (1); on 15 May 1892 (1); on 17 Sep. 1893 (1); on 18 Mar. 1900 (1); on 5 Mar. 1902 (1); 1491 (1). Woronow 3020 (6b). Worthington 7679 (1). Wright (A. H.) & Wright (A. A.) on 8 July 1925 (1). Wynd & Müller (C.) 349 (8).

Yatskievych (G.) 78–361 (1); 83–161 (1). Yatskievych (G.) & Forbes 82–211 (1). Yatskievych (G.) & Gastony 86–250 (8); 86–329 (5); 89–218 (8). Yatskievych (G.) & González L. 85–209 (7). Yatskievych (G.), Hevly & Windham 81–313 (1). Yatskievych (G.) & McCrary 85–05 (8); 86–13 (5); 86–30 (5); 86–31 (4); 86–31a (hybrid of 4 × 5). Yatskievych (G.), McCrary & Worthington 84–67 (1); 84–68(1). Yatskievych (G.), Ranker, González L., Starr (G.) & Starr (C.) 85–139 (7); 85–182 (2); 85–186 (6b); 85–211 (6a). Yatskievych (G.) & Windham 85–296 (1). Yatskievych (G.), Windham & Ranker 83–299 (8); 83–353 (6b); 84–04 (8). Yatskievych (G.), Windham, Ranker & Hallberg 83–467 (5). Yatskievych (G.), Windham & Sullivan 83–10 (1). Yatskievych (G.) & Wollenweber 83–87 (8); 83–128 (6b); 83–158 (6b). Yatskievych (G.) & Yatskievych (U.) 82–273 (1). Young on 4 Sep. 1915 (8).

Zolá B. 00710 (6b); 00742 (6b).

REVISIÓN DE LAS ESPECIES AMERICANAS DE *PANICUM* SUBGÉNERO *PANICUM* SECCIÓN *PANICUM* (POACEAE: PANICOIDEAE: PANICEAE)[1]

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Resumen

En el presente tratamiento se realiza una revisión de las especies americanas de la sección *Panicum* del género *Panicum*. Se estudiaron treinta y un especies de esta sección, incluyendo el análisis exomofológico y anatómico de las mismas. La sección *Panicum* se caracteriza por incluir especies anuales y perennes, que habitan en lugares abiertos y secos; las plantas poseen lígulas membranáceo-ciliadas, láminas oblongo-lanceoladas a filiformes, inflorescencias laxas y difusas, con espiguillas solitarias dispuestas sobre pedicelos usualmente largos; las espiguillas son ovoides a largamente elipsoides, glabras, con la gluma inferior (⅓–)½–¾(–⅞) del largo de la espiguilla, gluma superior y lemma inferior subiguales, pálea inferior tan larga como el antecio superior a reducida o ausente, flor inferior ausente, antecio superior crustáceo, y un número básico de cromosomas de $x = 9$. Desde el punto de vista histofoliar, dos patrones anatómicos distintivos fueron hallados en el transcorte de las especies de la sección. Se discuten las relaciones de la sección estudiada con otras del subgénero *Panicum*, como así también con géneros afines de la tribu Paniceae. Se incluye una clave de las especies analizadas, una descripción anatómica de la sección, fotografías de diez especies, descripciones morfológicas, ilustraciones y mapas de distribución de los diferentes taxones.

Abstract

Panicum subg. *Panicum* sect. *Panicum* is revised. Thirty-one American species are treated in this work, in which exomorphological and anatomical characters are considered. Section *Panicum* is defined mainly as an annual or perennial species of open and dry places, with membranous-ciliate ligules, leaves oblong-lanceolate to filiform, inflorescences lax and diffuse, with spikelets solitary on pedicels that are usually long; spikelets ovoid to long ellipsoid, glabrous, and the lower glume (⅓–)½–¾(–⅞) the length of the spikelet, upper glume and lower lemma subequal, lower palea as long as the upper anthecium to reduced or absent, lower flower absent, upper anthecium indurate, and a basic chromosome number of $x = 9$. Two anatomical patterns were found in the transverse section of the leaves. Possible relationships of *Panicum* with other sections of the typical subgenus, as well with other genera of the Paniceae, are discussed. A key to the species as well as an anatomical description of the section and photomicrographs of ten species, morphological descriptions of the species, illustrations, and distribution maps are presented.

El género *Panicum* L. es uno de los más grandes de la familia Poaceae, contando con aproximadamente 470 especies distribuidas en regiones cálidas y templadas del globo (Clayton & Renvoize, 1986). Dentro de este género la sección típica es cosmopolita, hallándose en América, Europa, Africa, Asia y Oceanía. Las especies de esta sección fueron tratadas por diferentes autores bajo varios nombres. Así Nees (1829) ubica a especies de este grupo en la sección *Effusa*. Steudel (1855) las agrupa en las secciones *Miliaria* y *Virgata*, Bentham (1878) en la serie *Paniculatae* y Hackel (1887) en la sección *Eupanicum*. Nash (1903) reconoce Capillaria, sin aclarar su rango taxonómico, incluyendo en el mismo especies anuales o perennes del sur de los Estados Unidos; trata dentro del mismo a *P. capillare* L., *P. capillarioides* Vasey, *P. cognatum* Schult. (= *Digitaria cognata* (Schult.) Pilg.), *P. diffusum* Sw., *P. filipes* Scribn., *P. flexile* (Gatt.) Scribn., *P. hallii* Vasey, *P. miliaceum* L., *P. philadelphicum* Bernh. ex Trin., *P. proliferum* Lam. (= *P. dichotomiflorum* Michx.) y *P. stenodes* Griseb.

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(especie de la sección *Tenera* (Hitchc. & Chase) Pilg). Más recientemente, Hitchcock y Chase (1910) consideran, en su revisión de las especies de *Panicum* de América del Norte, a las especies en los grupos Capillaria y Diffusa, agrupando en el primero a los taxones anuales y en el segundo a las especies perennes: consideran a *P. barbipulvinatum* Nash, *P. capillare*, *P. cayennense* Lam. (especie de la sección *Rudgeana* (Hitchc. & Chase) Zuloaga (Zuloaga, 1987b)), *P. decolorans* Hitchc. & Chase, *P. flexile*, *P. gattingeri* Nash, *P. hirticaule* J. Presl, *P. miliaceum*, *P. pampinosum* Hitchc. & Chase, *P. parcum* Hitchc. & Chase, *P. philadelphicum*, *P. sonorum* Beal y *P. stramineum* Hitchc. & Chase dentro de Capillaria y las siguientes especies en Diffusa: *P. capillarioides*, *P. diffusum*, *P. filipes*, *P. ghiesbreghtii* E. Fourn., *P. hallii*, *P. hirsutum* Sw. y *P. lepidulum* Hitchc. & Chase. Fernald (1919) realiza un estudio de grupo Capillaria para Nueva Inglaterra, considerando en el mismo a *P. capillare*, *P. philadelphicum* y *P. tuckermanii* Fernald. Stapf (1920) ubica las especies en la sección *Miliaceae*, tratando 11 especies para la flora de Africa tropical. Pilger (1931, 1940) trata a las especies dentro de la sección *Virgata* Hitchc. & Chase e incluye dentro de la misma a las secciones *Diffusa* de Hitchcock & Chase, *Hiantia* y *Miliacea* de Stapf. Henrard (1941) realiza una sinopsis del grupo Diffusa e incluye en el mismo a *P. bergii* Arechav., *P. campestre* Nees ex Trin. (especie de la sección *Rudgeana*, Zuloaga, 1987b), *P. capillarioides*, *P. ghiesbreghtii*, *P. hirsutum*, *P. peladoense* Henrard, *P. pilcomayense* Hack. (= *P. bergii*), *P. quadriglume* (Döll) Hitchc. y la especie asiática *P. trypheron* Schult.; caracteriza a este grupo por incluir especies perennes, cespitosas y con panojas difusas. Fairbrothers (1953, 1954) revisa las especies anuales del grupo y reconoce como especies válidas a *P. capillare*, *P. cayennense*, *P. decolorans*, *P. flexile*, *P. hillmanii* Swallen, *P. hirticaule*, *P. litophilum* Swallen, *P. miliaceum*, *P. parcum*, *P. philadelphicum* (con tres subespecies) y *P. stramineum*. Swallen (1943) considera para Panamá a las siguientes especies: *P. ghiesbreghtii*, *P. hirsutum* y *P. hirticaule*. Swallen (1955) incluye en su tratamiento de las gramíneas de Guatemala a *P. furvum* Swallen, *P. hirsutum*, *P. hirticaule*, *P. lepidulum*, *P. pampinosum* y *P. parcum*. Hsu (1965) ubica a diversas especies de estos grupos en la sección *Panicum*. Waller (1976) estudió las especies de la sección Diffusa que crecen en América del Norte e incluyó en su tratamiento a *P. capillarioides*, *P. diffusum*, *P. furvum*, *P. ghiesbreghtii*, *P. hallii* var. *filipes* (Scribn.) F. R. Waller, *P. hallii* var. *hallii*, *P. hirsutum*, *P. lepidulum*, *P. pilcomayense* y *P. tamaulipense* F. R. Waller & Morden. McVaugh (1983) describe en la *Flora Novo-Galiciana* a *P. hirsutum*, *P. hirticaule*, *P. lepidulum*, *P. parcum* y *P. stramineum* (con 3 variedades: var. típica, *miliaceum* e *hirticaule*). Zuloaga (1987a) efectúa una clasificación infragenérica de las especies americanas del género, considerando dentro de la sección típica a Capillaria y Diffusa e incluyendo en la misma a 22 especies. Davidse (1994) trata en la *Flora Mesoamericana* a. *P. furvum*, *P. ghiesbreghtii*, *P. hirsutum*, *P. hirticaule*, *P. hispidifolium*, *P. parcum* y *P. stramineum*. Tovar (1993), al describir las especies de gramíneas del Perú cita a *P. hirticaule*, *P. quadriglume* y *P. stramineum*.

El presente trabajo tiene por objetivo efectuar un estudio taxonómico y anatómico de las especies americanas de la sección *Panicum*, dilucidar las especies que integran la misma, discutir las relaciones específicas y de la sección con otros taxones infragenéricos de *Panicum*.

Materiales y Métodos

Para el estudio histofoliar se obtuvieron cortes transversales y epidermis a la altura del tercio medio de la penúltima lámina de la innovación fértil. Se utilizó material proveniente de ejemplares de herbario, previamente tratado con Contrad 70 (Schmid & Turner, 1977) durante 24 a 48 hs a 20°C, o material fresco fijado en FAA. Los cortes transversales se hicieron a mano alzada, previo tratamiento con HF al 5% durante 24 hs. Para la obtención de las epidermis se siguió el método de Metcalfe (1960).

Los cortes fueron coloreados con azul de metileno al 1% y con safranina al 1% en alcohol 80° o con safranina-alcian blue y montados en gelatina-glicerina.

Para la observación de las células clorenquimáticas se realizaron macerados siguiendo el método de Jeffrey (Sass, 1940). Para la identificación de los cuerpos de sílice y células suberosas se utilizó respectivamente fenol líquido (Metcalfe, 1960) y Sudán III (Sass, 1940). La determinación de los plástidos de almidón, y su distribución, se realizó mediante unas gotas de solución iodo-iodurada (Sass, 1940).

Para las descripciones histofoliares se adoptó la terminología propuesta por Ellis (1976, 1979).

Las observaciones anatómicas fueron hechas con un microscopio fotónico Wild M20 con cámara de dibujo. Las disecciones fueron estudiadas con un microscopio estereoscópico Wild M5 con cámara de dibujo.

El estudio exomorfológico fue realizado sobre la

base de materiales pertenecientes a los siguientes herbarios: B, BA, BAA, BLA, CEN, CEPEC, COL, CORD, CTES, F, G, GH, IAN, IBGE, ISC, JEPS, K, LA, LIL, LP, LPB, M, MEXU, MO, MY, NY, P, PORT, R, RB, S, SI, SP, UB, US, USM, UTMC, VEN, W, WIS, citados conforme a las siglas que figuran en Holmgren et al. (1990). Dentro del material examinado de cada especie sólo se citaron ejemplares representativos de cada país; una lista completa de los especímenes estudiados se encuentra ordenada alfabéticamente por coleccionista al final del texto (Apéndice).

Las fotomicrografías fueron tomadas con un equipo automático Nikon FXA, con cámara fotográfica DX-DB2 35 mm, y la película utilizada Kodak T-MAX de 100 ASA.

Para la obtención de fotomicrografías de epidermis abaxiales de la lemma y pálea del antecio superior se empleó un microscopio electrónico de barrido Jeol JSM-25 SII, perteneciente a la Facultad de Odontología (Universidad Nacional de Buenos Aires, Argentina).

Con un asterisco (*) se señalan en la cita de materiales examinados los ejemplares empleados en el estudio histofoliar. Con dos asteriscos (**) se indican aquellos especímenes utilizados en el análisis de la lemma y pálea superior.

Se presentan fotomicrografías MEB (Figs. 1, 2) en la descripción de la morfología; mapas de distribución (Figs. 3–11) en Distribución y Ecologia; transcortes (Figs. 12–14) en Anatomía Foliar y Discusión; e ilustraciones de las especies de *Panicum* secc. *Panicum* (Figs. 15–28) en el Tratamiento Taxonómico.

Morfología

Hábito

Dentro de esta sección se incluyen especies anuales y perennes. El tamaño de las plantas es variable, desde especies de 2–8 cm de alto, como *P. mohavense* Reeder (Fig. 25G–N), hasta otras que alcanzan aproximadamente los 2–3 m de altura, como por ejemplo *P. hirsutum* (Fig. 21). Todas las especies son cespitosas, con cañas simples o ramificadas en los nudos basales y medios, excepcionalmente con ramificaciones libres en la porción superior de las cañas en *P. aquarum* Zuloaga & Morrone (Fig. 16); las cañas son multinodes, con entrenudos muy cortos hacia la base y alargados en las ramas floríferas o paucinodes, con 1–2 nudos en *P. mohavense*; los entrenudos son cilíndricos, huecos y pilosos a glabros. Los nudos son normalmente comprimidos, castaños a oscuros y con pilosidad variable. Las vainas son abiertas y estriadas y varían desde glabras a densamente pilosas con pilosidad variable, con pelos tuberculados o sin los mismos (urticantes en *P. hirsutum*) o glaucas como en *P. hallii* var. *hallii, P. hallii* var. *filipes* y *P. tamaulipense*; excepcionalmente las vainas son esponjosas, con aerénquima, en *P. aquarum*. Las lígulas son membranáceas en la porción basal y corta a largamente pestañosas hacia la porción distal. Las láminas son planas, o con los bordes involutos, y varían en forma desde oblongo-lanceoladas, lanceoladas, linear-lanceoladas, lineares a filiformes; la pilosidad en las láminas es variable, desde híspidas o hirsutas, con pelos tuberculados, a glabras, siendo los bordes escabrosos, los basales con pelos tuberculados o sin los mismos. En *P. hallii* var. *hallii, P. hallii* var. *filipes* y *P. tamaulipense* las láminas inferiores a la senescencia persisten enrolladas en la base de la planta. La persistencia de hojas basales enrolladas fue previamente citada en *Panicum mystasipum* Zuloaga & Morrone (Zuloaga & Morrone, 1992); estos autores sugieren que posiblemente este carácter se encuentre relacionado con la protección de las yemas a factores ambientales externos.

Inflorescencias

Las especies de esta sección poseen panojas terminales o terminales y axilares. El primer caso se da en las especies perennes, las que poseen una caña florífera con una inflorescencia terminal. En las especies anuales, por el contrario, se encuentran inflorescencias terminales en las cañas principales y de las ramificaciones basales salen a su vez inflorescencias axilares. Excepcionalmente se observa un patrón complejo de ramificación en la inflorescencia de *P. aquarum* (Zuloaga & Morrone, 1991).

Las inflorescencias son laxas y difusas, con espiguillas solitarias, en la mayoría de las especies, a espiciformes a subespiciformes, con las ramificaciones adpresas al eje principal, en *P. decolorans, P. chasei* Roseng., B. R. Arrill. & Izag., *P. magnispicula* Zuloaga, Morrone & Valls (Fig. 24) y *P. pampinosum*. Las ramificaciones inferiores de la inflorescencia son verticiladas en *P. bergii* (Fig. 18) y *P. hillmanii* (ocasionalmente verticiladas en ejemplares de *P. capillare*) y alternas a subopuestas en el resto de los taxones. Además, en *P. bergii* y *P. capillare* las inflorescencias son caedizas en su conjunto a la madurez, actuando la panoja como una unidad de dispersión.

Vegetti & Pensiero (1993) estudian la tipología de diversas especies de la sección *Panicum*, concluyendo que la inflorescencia en este grupo es po-

litélica, con florescencia principal desarrollada, no truncada.

ESPIGUILLAS

Las espiguillas son bifloras, con un antecio inferior estéril y uno superior perfecto, a excepcionalmente trifloras, con dos antecios inferiores estériles y uno superior perfecto en *P. quadriglume* (Fig. 27). Las especies de esta sección poseen espiguillas globosas u ovoides a largamente elipsoides, cerradas (abiertas a la madurez en *P. aquarum*, *P. aztecanum* Zuloaga & Morrone, *P. ephemeroides* Zuloaga & Morrone, *P. exiguum* Mez, *P. hispidifolium* Swallen, *P. lepidulum*, *P. magnispicula*, *P. peladoense* y *P. quadriglume*), glabras y pajizas o con tintes purpúreos. La gluma inferior varía en tamaño desde ½–¾(–⅘) del largo de la gluma superior y la lemma inferior (midiendo de ⅓ a ½ en *P. flexile*, *P. mohavense* y *P. stramineum*); es aguda a acuminada, 3–5-nervia, ocasionalmente 7–9-nervia, con el nervio medio a menudo escabroso. La gluma superior y lemma inferior son subiguales y 7–9(13–15)-nervias, ocasionalmente 5–7-nervias en *P. aquarum* y *P. ephemeroides*; la gluma inferior y superior se encuentran separadas por un entrenudo marcado en *P. aquarum* (Fig. 16), *P. aztecanum* (Fig. 17) y *P. parcum*. La gluma superior es tempranamente caediza en un grupo de especies que incluye a *P. exiguum*, *P. furvum*, *P. peladoense* y *P. quadriglume*. Este carácter está correlacionado con el hecho de poseer estas especies antecio superior negruzco a la madurez, el que queda expuesto por la caída de la gluma superior. La pálea inferior varía en su desarrollo, desde especies en que la misma es nula o poco manifiesta, como por ejemplo *P. capillare* o *P. hirticaule* hasta especies en las que alcanza el mismo largo que la lemma inferior, como es el caso de *P. bergii*, *P. chasei* y *P. stramineum*. La flor inferior está ausente. El antecio superior encierra una flor perfecta; la lemma y pálea están endurecidas y poseen un color pajizo a castaño, en especies como *P. chasei* o negruzco, tal como se mencionó anteriormente para *P. exiguum*, *P. peladoense* y especies relacionadas. La lemma encierra a la pálea y es 5–7-nervia; la pálea es 2-nervia. En el interior del antecio se encuentran dos lodículas truncadas, cuneiformes, que abrazan los bordes inferiores de la pálea superior, tres estambres y un ovario con dos estilos libres desde la base y estigmas plumosos. Finalmente el cariopsis varía de ovoide a elipsoide o fusiforme, tiene un hilo punctiforme y el embrión alcanza aproximadamente ⅓ a ½ del largo de la cariopsis (de ½ a ¾ en *P. capillarioides* y *P. decolorans*).

La espiguilla de las especies aquí tratadas posee el plan estructural de las Paniceae, pero difiere por tener una zona de articulación primaria en la base del antecio superior, cayendo este último desnudo a la madurez, desarticulando posteriormente las restantes brácteas en la base de la gluma inferior junto al pedicelo. La presencia de desarticulación primaria en la base del antecio superior ha sido previamente señalada en la tribu Paniceae en *Axonopus*, *Brachiaria*, *Echinolaena*, *Ichnanthus*, *Melinis*, *Panicum*, *Paspalum*, *Pennisetum*, *Rhynchelytrum*, *Sacciolepis*, *Tricholaena* y *Yakirra* (Lazarides & Webster, 1984; Silberbauer-Gottsberger, 1984; Davidse, 1987; Webster, 1987; Zuloaga, 1987a; Morrone & Zuloaga, 1992; Morrone et al., 1995).

TEXTURA Y ORNAMENTACIÓN DEL ANTECIO SUPERIOR

El antecio superior es ovoide a largamente elipsoide (obovoide en *P. alatum* Zuloaga & Morrone, Fig. 15) dorsiventralmente comprimido, crustáceo, liso y glabro, con los bordes de la lemma enrollados y cubriendo los ⅔ de la superficie de la pálea. La epidermis abaxial de la lemma y pálea posee células largas rectangulares distribuidas en hileras longitudinales, más de tres veces más largas que anchas, de paredes anticlinales longitudinales onduladas.

La epidermis abaxial puede presentar, en particular sobre la pálea, diferentes ornamentaciones, incluyendo papilas simples, papilas verrugosas, micropelos y aguijones.

La epidermis de la lemma comúnmente no posee ornamentación, habiéndose observado papilas simples distribuidas regularmente en toda la superficie en *Panicum alatum* var. *alatum* (Fig. 1C), *P. hirticaule* var. *verrucosum* Zuloaga & Morrone (Fig. 1A) y *P. magnispicula* y en ejemplares aislados de *P. stramineum* (como por ejemplo en *Palmer 206*) o sólo junto a la porción distal de la lemma en *P. quadriglume* (Fig. 2C).

Papilas simples distribuidas irregularmente en el ápice de la pálea se observaron en *Panicum alatum* var. *longiflorum* Zuloaga & Morrone, *P. alatum* var. *minus* (Andersson) Zuloaga & Morrone, *P. aztecanum* Zuloaga & Morrone, *P. bergii*, *P. capillare*, *P. chasei*, *P. diffusum* (Fig. 2A), *P. exiguum*, *P. flexile*, *P. furvum* (Fig. 2D), *P. ghiesbreghtii*, *P. hallii* (Fig. 2E), *P. hirsutum*, *P. hirticaule* var. *hirticaule*, *P. hispidifolium* (Fig. 2G), *P. lepidulum* (Fig. 2F), *P. mohavense*, *P. mucronulatum* Mez, *P. pampinosum*, *P. peladoense*, *P. philadelphicum*, *P. quadriglume* (Fig. 2B, C) y *P. stramineum*. Papilas simples distribuidas regularmente en toda la superficie de la pálea se hallaron en *P. alatum* var. *alatum* (Fig. 1C, D),

P. hirticaule var. *verrucosum* (Fig. 1A, B), *P. magnispicula* y ocasionalmente en ejemplares de *P. stramineum* (Fig. 1H). Papilas verrugosas agrupadas irregularmente en el ápice de la pálea se hallaron en *P. aquarum*, *P. capillarioides*, *P. decolorans* (Fig. 2H), *P. ephemeroides*, *P. hillmanii*, *P. hispidifolium* (Fig. 2G), *P. miliaceum* y *P. parcum*.

Se encontraron aguijones en el ápice de la lemma junto a la pálea en *Panicum alatum* var. *minus*, *P. bergii*, *P. ghiesbreghtii*, *P. lepidulum*, *P. miliaceum* y *P. mucronulatum*.

Micropelos bicelulares, con célula distal globosa, se observaron en el ápice de la pálea de *Panicum aztecanum*, *P. ghiesbreghtii*, *P. lepidulum* y *P. mucronulatum*.

La base del antecio difiere en las especies estudiadas. Así, *Panicum aquarum*, *P. aztecanum*, *P. decolorans*, *P. ephemeroides*, *P. hispidifolium* (Fig. 1G), *P. lepidulum*, *P. magnispicula* y *P. parcum* poseen un anillo compuesto de células menos engrosadas que el resto de la superficie de la lemma, notablemente castaño a la madurez. Este anillo es menos manifiesto en *P. capillare*, *P. flexile* y *P. philadelphicum*. En *Panicum bergii*, *P. capillarioides*, *P. diffusum*, *P. exiguum*, *P. furvum*, *P. ghiesbreghtii*, *P. hallii*, *P. hillmanii*, *P. hirsutum*, *P. hirticaule* (Fig. 1B, F), *P. miliaceum*, *P. mohavense*, *P. mucronulatum*, *P. pampinosum*, *P. peladoense*, *P. quadriglume* y *P. stramineum* (Fig. 1H) se encuentran 2 cicatrices basales a ambos márgenes de la lemma, compuestas de células de paredes delgadas, menos engrosadas que el resto de la superficie de la lemma, y marcadamente castañas a la madurez. *Panicum alatum* difiere de las restantes especies por poseer 2 expansiones aliformes, carnosas en los márgenes basales de la lemma, oliváceas a la madurez (Fig. 1D, E); este carácter es, hasta el momento, único dentro del género *Panicum* y se encuentra, dentro de la tribu Paniceae, presente en los géneros *Ichnanthus* P. Beauv. y *Echinolaena* Desv. A través de un análisis con Sudán IV (Jensen, 1962) se determinó en *P. alatum* la presencia de aceites en los apéndices carnosos. La presencia de eleosomas en gramíneas fue correlacionada con la dispersión a través de hormigas (mirmecofilia), habiendo sido previamente mencionada en diversos géneros de gramíneas por Berg (1985), Davidse (1987), Zuloaga et al. (1988) y Morrone & Zuloaga (1991).

Distribución y Ecología

Las especies de la sección *Panicum* se encuentran aproximadamente desde los 50° de latitud norte hasta los 40° de latitud sur, desde el SE de Canadá y los Estados Unidos de América hasta la región central de Chile y Argentina (Figs. 3–11). Entre los taxones con distribución más amplia dentro de la sección se encuentran: *Panicum stramineum*, desde el SW de los Estados Unidos de América y México, Islas del Caribe hasta el W de Argentina; *P. alatum* var. *minus* desde el SW de Estados Unidos de América hasta Venezuela y Ecuador (en las Islas Galápagos), *P. hirticaule* var. *hirticaule* desde el SW de Estados Unidos de América hasta Venezuela, Ecuador y Perú, *P. ghiesbreghtii* desde el SW de Estados Unidos de América, México, Islas del Caribe hasta Venezuela, Colombia y Ecuador. *Panicum hirsutum* se extiende desde el SW de Estados Unidos de América, México e Islas del Caribe hasta Ecuador, Colombia, Venezuela y N de Brasil, habiendo sido coleccionada ocasionalmente en el N de Argentina. Finalmente, *P. hispidifolium* crece desde el sur de México hasta Colombia y Venezuela.

En América del Norte habitan exclusivamente las siguientes especies: *Panicum philadelphicum*, *P. flexile* y *P. capillare* se encuentran en el SE de Canadá y Estados Unidos de América, habiendo sido introducida *P. capillare* en América del Sur en Brasil, Uruguay, Argentina y Chile. *Panicum pampinosum* y *P. mohavense* son endémicas del SW de Estados Unidos de América, mientras que *P. alatum* var. *alatum*, *P. capillaroides*, *P. hallii* var. *hallii*, *P. hallii* var. *filipes*, *P. hillmanii* y *P. hirticaule* var. *verrucosum* crecen desde el S y SW de Estados Unidos de América hasta el NE y centro de México. Por último, *P. aztecanum*, *P. decolorans*, *P. alatum* var. *longiflorum* y *P. tamaulipense* son endémicas de México.

Panicum lepidulum y *P. parcum* son exclusivas de México y América Central y *P. furvum* y *P. diffu-*

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Figura 1. Fotomicrografías MEB de antecios superiores de especies de *Panicum*. A,B. *Panicum hirticaule* var. *verrucosum*.—A. Apice de la lemma y palea, con papilas.—B. Base del antecio superior, con dos cicatrices sobre la lemma. C,D. *Panicum alatum* var. *alatum*.—C. Ápice de la lemma y pálea.—D. Base del antecio, con dos expansiones carnosas sobre la lemma.—E. *Panicum alatum* var. *longiflorum*, base del antecio, con dos expansiones carnosas.—F. *Panicum hirticaule*, base del antecio, con dos cicatrices sobre la lemma.—G. *Panicum hispidifolium*, base del antecio superior, con un anillo basal.—H. *Panicum stramineum*, base del antecio, con dos cicatrices sobre la lemma. (A, B, *Colunga & Zizumbo 44*; C, D, *Wiggins 15160*; E, *Carter 4970*; F, *Pohl & Davidse 12177*; G, *Rodríguez 1981*; H, *Palmer 206*).

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sum son endémicas de Guatemala e Islas del Caribe respectivamente.

Nueve especies son exclusivas de América del Sur. Dentro de las mismas, las que poseen una distribución más amplia son *P. exiguum* y *P. bergii* var. *bergii,* habiendo sido introducida esta última especie en los Estados Unidos de América; *P. aquarum* se halla en el N y NW de América del Sur, *P. peladoense* en el S de Brasil, Bolivia, Paraguay y Argentina, *P. quadriglume* en Perú, Bolivia, Paraguay, Brasil y Argentina, *P. bergii* var. *pilosissimum* en el NE de Argentina y S de Brasil, *P. chasei* en el E de Argentina, S de Brasil y Uruguay y *P. mucronulatum, P. ephemeroides* y *P. magnispicula* son endémicas del Brasil.

Todas las especies de esta sección habitan usualmente en campos o sabanas, sobre suelos arcillosos, arenosos a rocosos, en bordes de caminos y también en laderas de montaña; algunas especies en América Central se hallan en bosques decíduos. Una excepción la constituye *P. aquarum,* especie que habita campos bajos inundables del norte de América del Sur. Las especies crecen desde el nivel del mar hasta los aproximadamente 1300 m, llegando *P. lepidulum* hasta los 2150 m y *P. hirticaule* hasta los 2500 m en el Perú.

Números Cromosómicos

Los estudios cariológicos en la sección *Panicum* son escasos, habiéndose registrado datos sobre la citología de 16 especies. La sección se caracteriza por tener un número básico de cromosomas $x = 9$ (Zuloaga, 1987a) y se han citado diferentes niveles de ploidía dentro de la misma.

A continuación se resumen los números cromosómicos determinados para las especies de la sección *Panicum* tratadas en el presente estudio:

Panicum alatum var. *minus*, $2n = 18$ (Gould, 1965, bajo *P. hirticaule*).

Panicum bergii var. *bergii*, $n = 18$ (Dubcovsky & Zuloaga, 1991); $2n = 36$ (Delay, 1950; Parodi, 1946, bajo *P. pilcomayense*; Núñez, 1952, bajo *P. pilcomayense*).

Panicum capillare, $n = 9$ (Spellenberg, 1967, bajo *P. capillare* var. *occidentale* Rydb.); $2n = 18$ (Avdulov, 1931; Gould, 1968, 1975; Spellenberg, 1970; Ferakova, 1976; Fairbrothers, 1954; Tzvelev, 1976, bajo *P. capillare* subsp. *barbipulvinatum* (Nash) Tzvelev; Reeder, 1977; Love & Love, 1981, bajo *P. capillare* var. *occidentale*; Vahidy et al., 1987).

Panicum capillarioides, $2n = 36$ (Gould, 1960, 1968).

Panicum decolorans, $2n = 36$ (Gould, 1966).

Panicum flexile, $2n = 18$ (Brown, 1948; Fairbrothers, 1954).

Panicum hallii var. *filipes*, $2n = 18$ (Brown, 1951; Gould, 1958, 1968; Waller, 1976); $2n = 36$ (Gould, 1958).

Panicum hallii var. *hallii*, $2n = 18$ (Gould, 1958, 1965, 1966, 1968; Reeder, 1971; Waller, 1976); $2n = 36$ (Waller, 1976, bajo *P. pilcomayense*).

Panicum hillmanii, $2n = 18$ (Fairbrothers, 1954).

Panicum hirticaule, $n = 9$ (Davidse & Pohl, 1972); $2n = 18$ (Fairbrothers, 1954; Gould, 1975).

Panicum hirsutum, $2n = 36$ (Gould, 1975; Waller, 1975, 1976).

Panicum hispidifolium, $n = 27$ (Dubcovsky & Zuloaga, 1991).

Panicum miliaceum, $n = 18$ (Parfitt, 1981); $2n = 36$ (Avdulov, 1931; Krishnaswamy, 1951; Frey et al., 1981), $2n = 54$ (Krishnaswamy, 1951); $2n = 72$ (Arenkova, 1940; Krishnaswamy, 1951).

Panicum pampinosum, $2n = 18$ (Reeder, 1977); $2n = 36$ (Gould, 1966).

Panicum parcum, $2n = 36$ (Gould, 1966; Gould & Soderstrom, 1970).

Panicum philadelphicum, $2n = 18$ (Brown, 1948; Fairbrothers, 1954, bajo *P. lithophilum*).

Panicum stramineum, $2n = 36$ (Fairbrothers, 1954).

Anatomía Foliar

Caracteres histofoliares en corte transversal (Fig. 12). *Transcorte*: plano, expandido o en forma de "U" o "V"; semiláminas simétricas a ambos lados del nervio medio; láminas de ancho variable, con 16–120 haces vasculares en transcorte; espesor de la lámina variable, de 91–250(–325) μm en las

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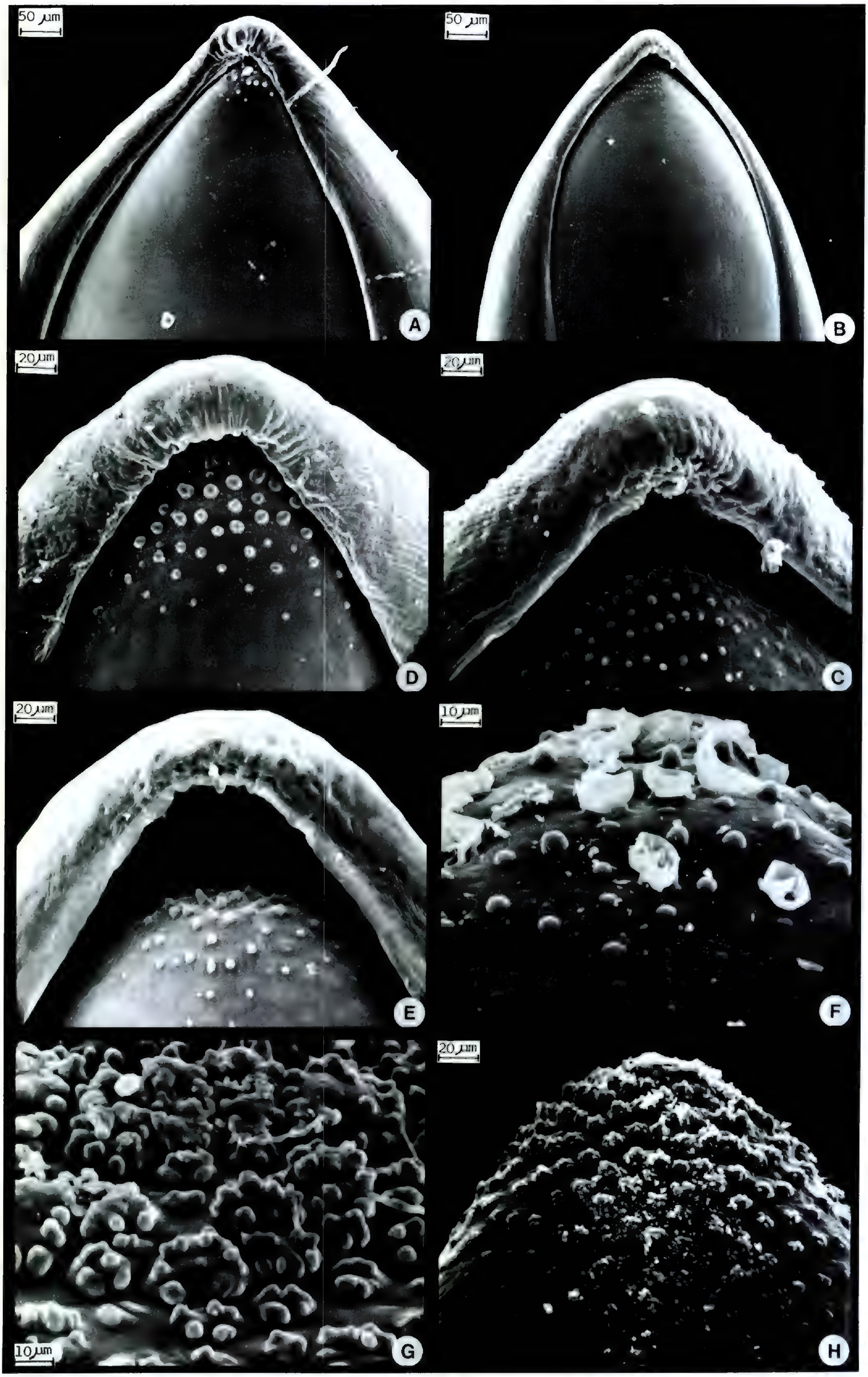
Figura 2. Fotomicrografías MEB de antecios superiores de especies de *Panicum*.—A. *Panicum diffusum*. Ápice de la lemma y pálea, con papilas simples hacia el ápice de la pálea. B, C. *Panicum quadriglume*.—B. Apice de la lemma y pálea.—C. Detalle de B, con papilas simples.—D. *Panicum furvum*. Apice de la lemma y pálea, con papilas hacia el ápice de la pálea.—E. *Panicum hallii* var. *hallii*. Apice de la lemma y pálea, con papilas sobre la pálea.—F. *Panicum lepidulum*. Apice de la pálea, con papilas simples y micropelos.—G. *Panicum hispidifolium*. Apice de la pálea, con papilas verrugosas.—H. *Panicum decolorans*. Apice de la palea, con papilas verrugosas. (A, *Eggers 76*; B, C, *Chase 8897*; D, *Steyermark 51627*; E, *Hall 816*; F, *Pringle 497*; G, *Rodríguez 1981*; H, *Humboldt s.n.*)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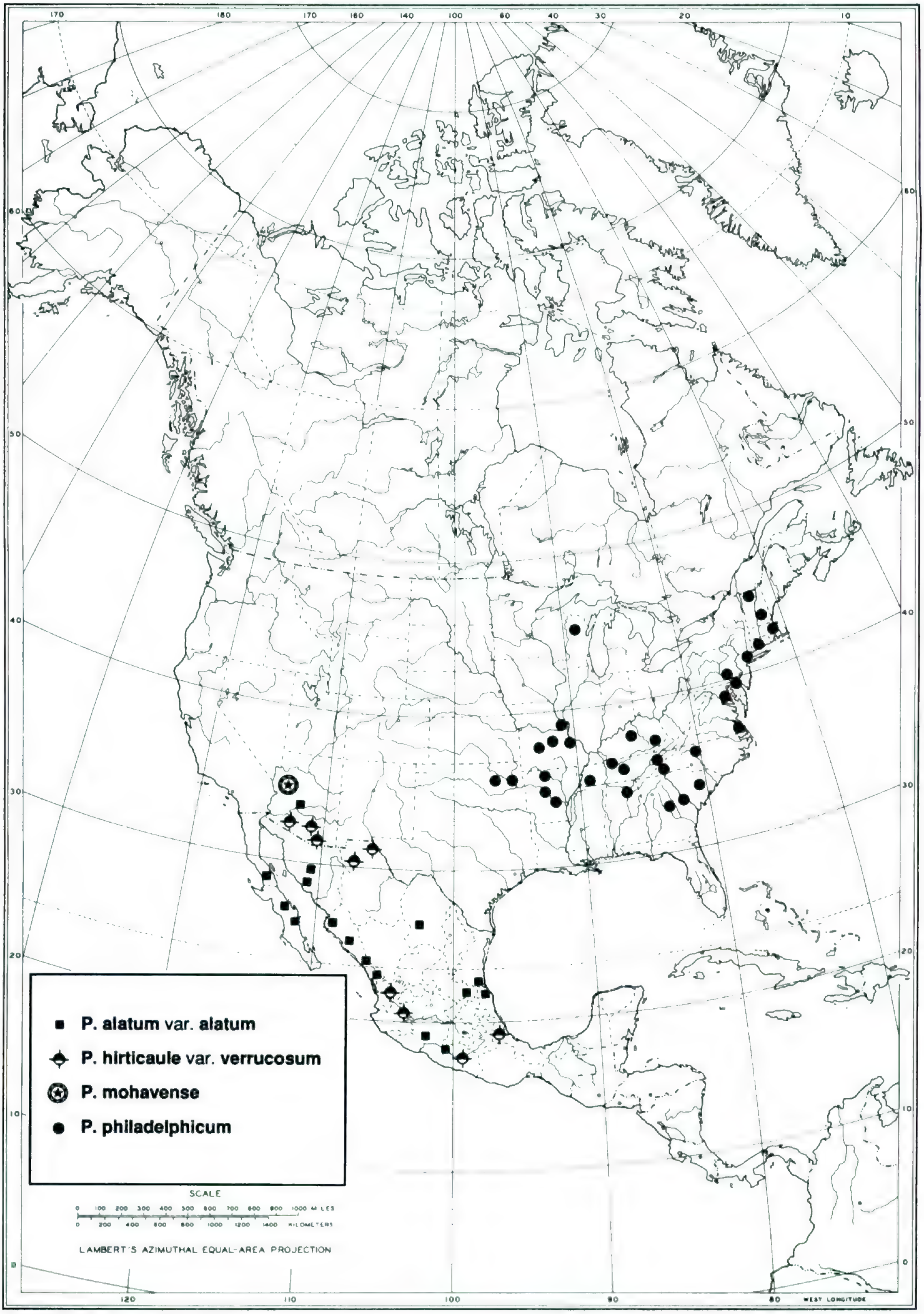


Figura 3. Distribución de *Panicum alatum* var. *alatum*, *P. hirticaule* var. *verrucosum*, *P. mohavense* y *P. philadelphicum*.

Figura 4. Distribución de *Panicum hirsutum*, *P. mucronulatum* y *P. peladoense*.

costillas, 40–170 μm en los surcos, los márgenes planos a ligeramente enrollados; superficie adaxial plana sin costillas y surcos manifiestos o con costillas de ápice redondeados a ligeramente aplanados y surcos poco profundos y suaves, hasta ⅓ del ancho del transcorte (en *P. aquarum*, *P. aztecanum* y *P. ephemeroides* con surcos profundos, hasta ½ del ancho del transcorte); costillas y surcos abaxiales variables, no manifiestos o con costillas de ápice redondeado a ligeramente plano y surcos suavemente pronunciados, hasta 1/6 del ancho del transcorte. *Haz vascular medio*: de estructura variable, con un haz vascular de primer orden estructuralmente indistinguible de los restantes laterales o con un haz vascular de primer orden estructuralmente distinguible, solitario o acompañado por 1–2 haces vasculares de primer orden y 2–5 haces vasculares de segundo orden y con células parenquimáticas incoloras localizadas hacia la cara adaxial. *Distribución de los haces vasculares*: 3–16 haces vasculares de primer orden (21–30 haces vasculares de primer orden en *P. hirsutum*), (2–)3–7 haces vasculares de segundo orden entre haces vasculares de primer orden contiguos; todos los haces vasculares equidistantes de ambas epidermis. *Estructura de los haces vasculares*: haces vasculares de primer orden de contorno subcircular a elípticos, con vasos de metaxilema de contorno angular y diámetro igual o menor que las células parenquimáticas Kranz; haces vasculares de segundo orden, de contorno angular, con xilema y floema distinguible. *Vaina de los haces vasculares*: vaina parenquimática externa Kranz de estructura variable: (A): de contorno regular, compuestas por células Kranz de paredes radiales y tangencial interna recta, con cloroplastos especializados, alargados, de posición centrípeta o (B) de contorno irregular con las paredes radiales y tangencial externa manifiestamente arqueadas y con cloroplastos especializados, discoides, localizados centrífugamente; exten-

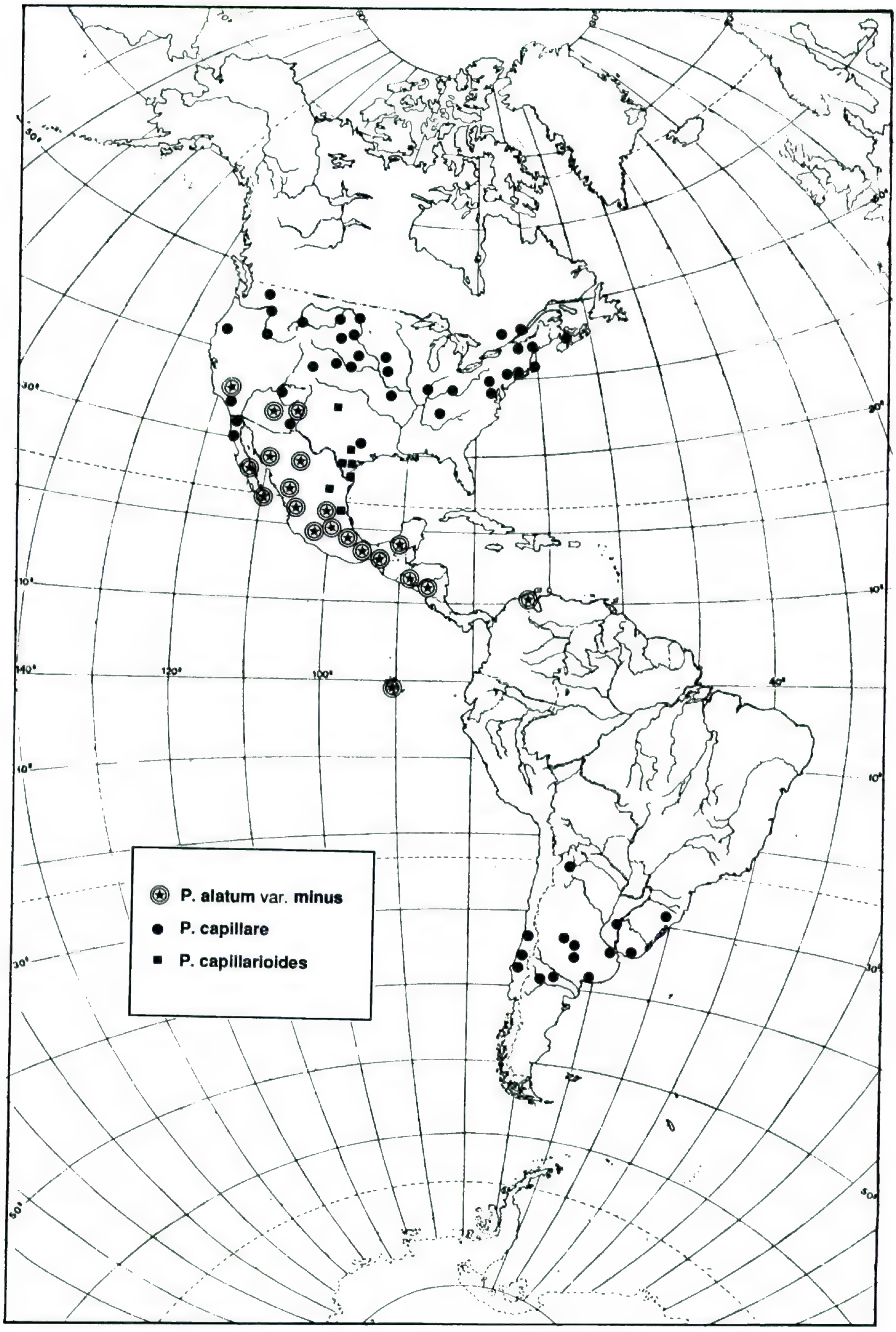


Figura 5. Distribución de *Panicum alatum* var. *minus*, *P. capillare* y *P. capillarioides*.

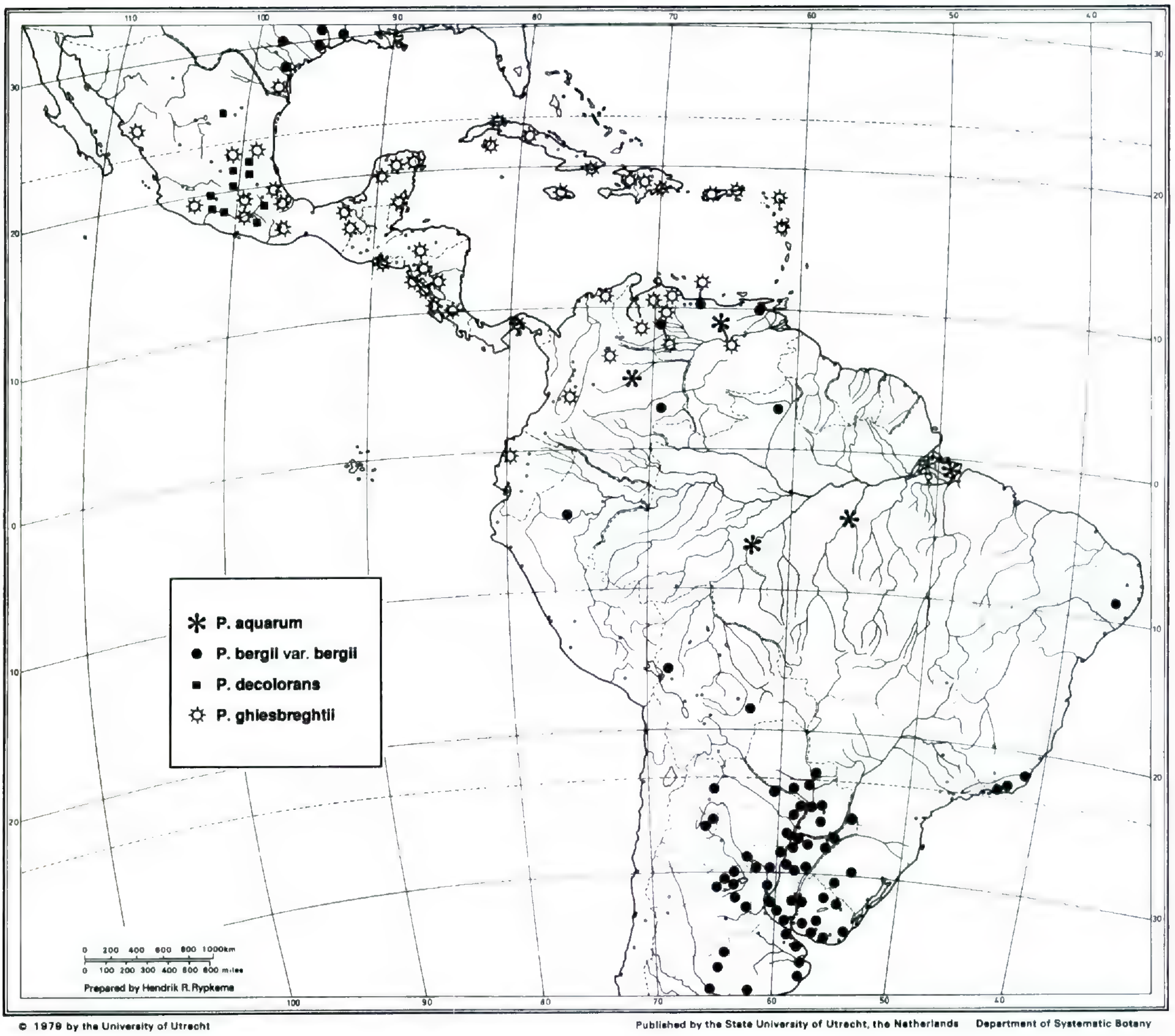


Figura 6. Distribucíon de *Panicum aquarum*, *P. bergii* var. *bergii*, *P. decolorans* y *P. ghiesbreghtii*.

siones parenquimáticas de la vaina ausentes; vaina interna mestomática completa, compuesta por células pequeñas de paredes uniformemente engrosadas. *Células distintivas Kranz*: ausentes. *Esclerénquima*: pobremente desarrollado, en grupos discontinuos, adaxiales y abaxiales, subepidérmicos, en contacto o no con los haces vasculares; margen de la lámina con escaso esclerénquima submarginal. *Mesófilo*: radiado en una capa contínua o interrumpida adaxial o abaxialmente por trabas de esclerénquima, compacto, con escasos espacios intercelulares; células clorenquimáticas tabulares; 2(–3) células clorenquimáticas entre haces vasculares contíguos; células parenquimáticas incoloras ausentes o presentes por debajo de las células buliformes, compuestas por 1–2–3-series células en contacto con ambas epidermis o sólo por debajo de las células buliformes, en *P. furvum*. "Arm cells" ausentes. Células fusoides ausentes. *Células epidérmicas adaxiales*: células buliformes presentes en los surcos adaxiales y entre los haces vasculares, en grupos pequeños, en forma de abanico, compuestos por 2–7 células, la central usualmente de mayor tamaño que las laterales, ocupando hasta ⅓ del ancho del transcorte. Células epidérmicas pequeñas y regulares en forma, excepcionalmente arqueadas en *P. aquarum*, *P. aztecanum* y *P. epheme-roides*. Aguijones y ganchos de frecuencia variable. Papilas ausentes, excepcionalmente presentes en ejemplares aislados de *P. stramineum*. Macropelos presentes o ausentes, cuando presentes con base bulbosa, asociada a células epidérmicas sobreelevadas o en el mismo nivel que el resto de la superficie. *Células epidérmicas abaxiales*: células buliformes ausentes. Células epidermicas pequeñas. Aguijones y ganchos como en la cara adaxial. Papilas ausentes. Macropelos de frecuencia variable, similares a los presentes en la cara adaxial.

Epidermis abaxial en vista paradermal (Fig.

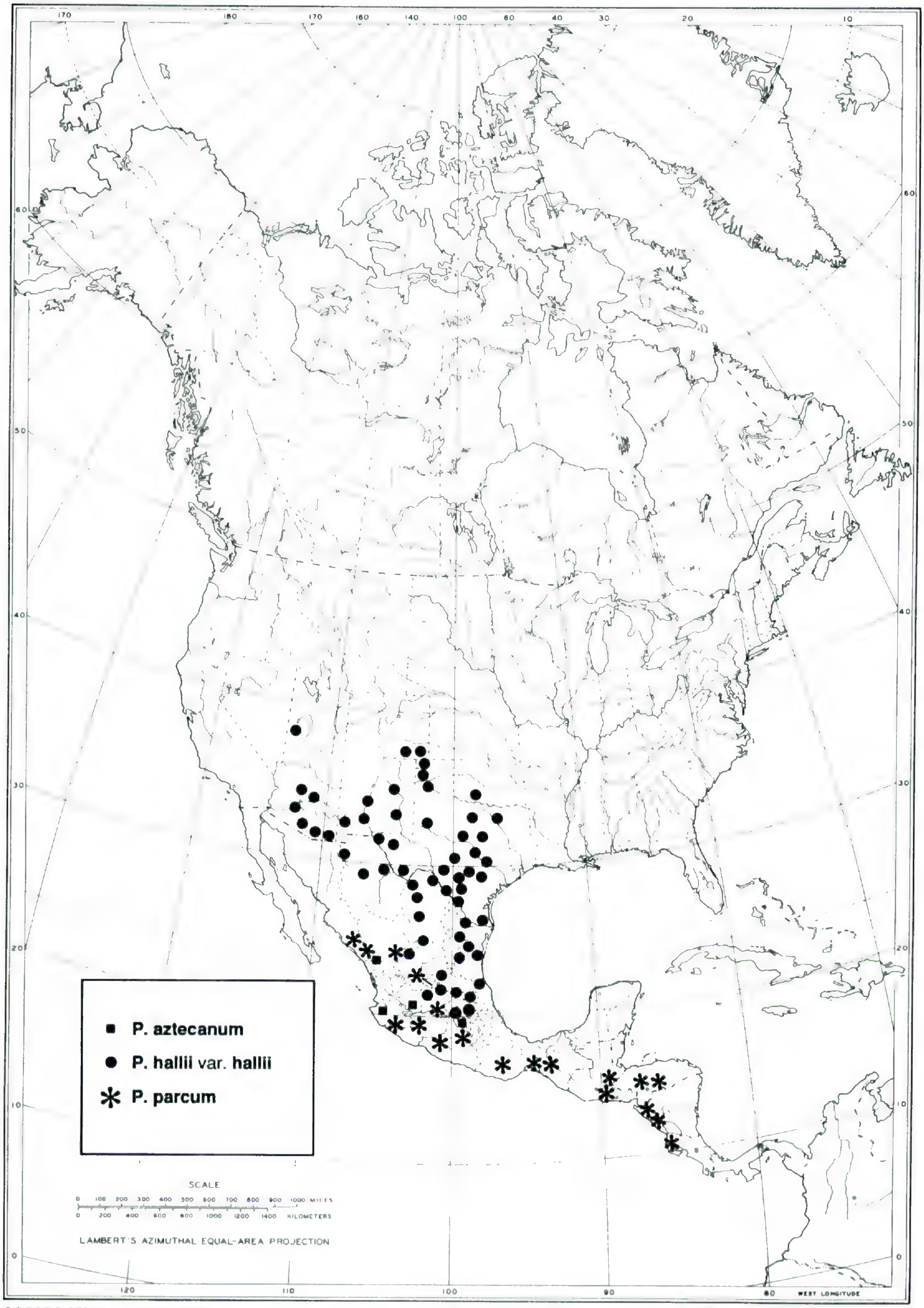


Figura 7. Distribución de *Panicum aztecanum*, *P. hallii* var. *hallii* y *P. parcum*.

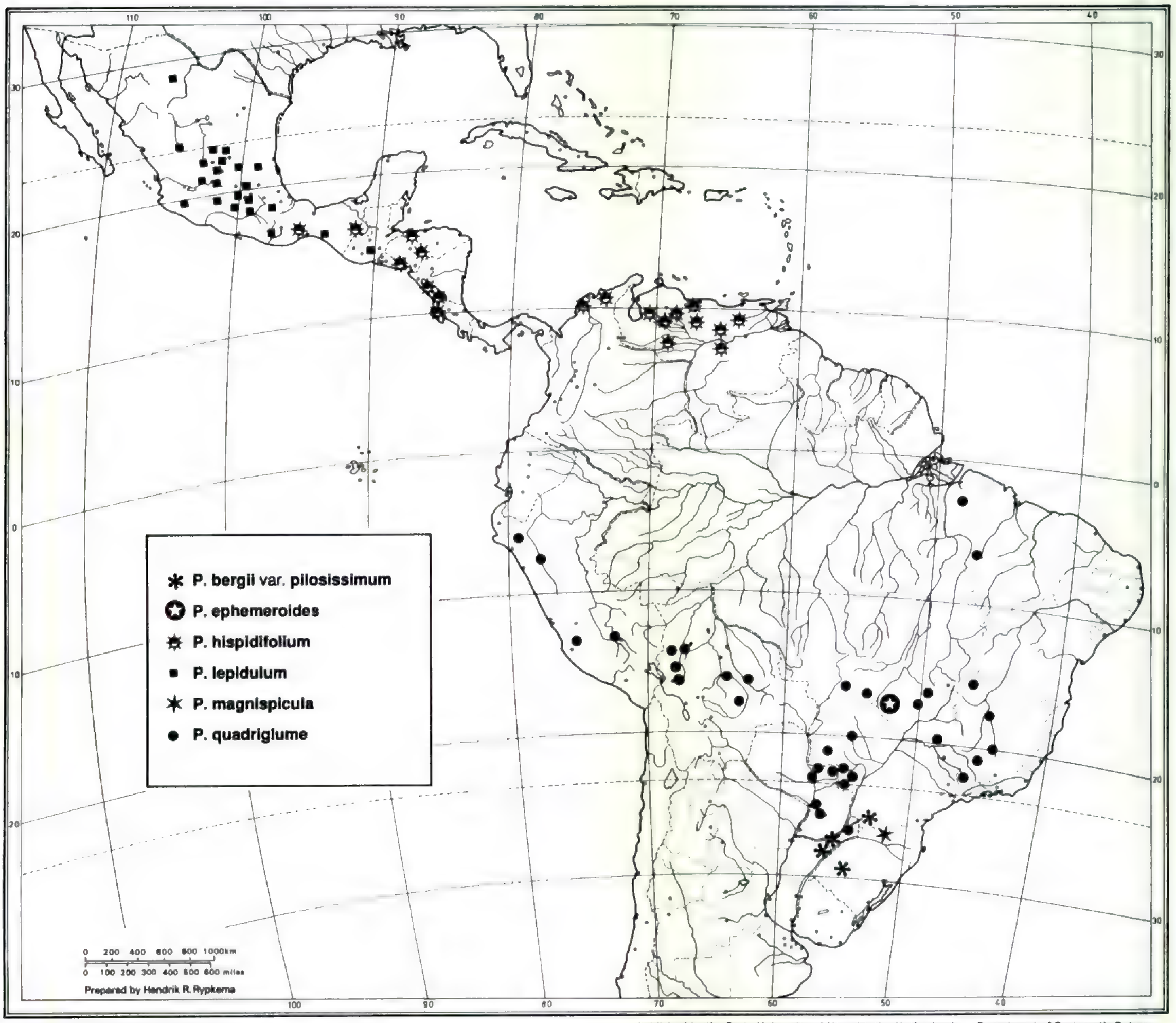


Figura 8. Distribución de *Panicum bergii* var. *pilosissimum*, *P. ephemeroides*, *P. hispidifolium*, *P. lepidulum*, *P. magnispicula* y *P. quadriglume*.

13). Zonación: zonas costales e intercostales diferenciadas; zonas costales 1–6 células de ancho; zonas intercostales de 3–14 células de ancho, homogéneas. *Células largas intercostales*: rectangulares, más de 3 veces más largas que anchas, de paredes suavemente engrosadas, las anticlinales longitudinales onduladas, paralelas, las anticlinales transversales rectas. *Células cortas intercostales*: con su eje mayor transversalmente alargado, solitarias o en pares sílico-suberosos, de distribución homogénea en la zona intercostal, alternando con 1(–2) células largas, o raro más. *Aparatos estomáticos*: de 26–40 µm de largo, 15.5–26 µm de ancho (19.5 y 45 µm de largo en *P. mohavense* y *P. hirsutum* respectivamente), distribuidos en 2 hileras longitudinales en la zona intercostal, cada una próxima a la zona costal, usualmente en 1 hilera, de disposición central en *P. peladoense*; estomas separados por una célula larga interestomática, rectangular, de paredes terminales cóncavas; células subsidiarias cupuliformes a ligeramente triangulares. *Micropelos*: bicelulares, fusiformes, de 45.5–78 µm de largo, comúnmente distribuidos en la región central de la zona intercostal, con la célula basal de paredes paralelas, más engrosadas que las de la célula distal; célula distal 2 a 3 veces más larga que la basal, decídua, de paredes muy delgadas (en *P. ephemeroides* y *P. magnispicula* la célula basal puede ser menor del mismo tamaño que la distal). *Aguijones*: presentes o ausentes, cuando presentes de frecuencia variable, distribuidos en las zonas costales, de barba más larga que la base. *Ganchos*: ausentes o presentes, de frecuencia variable, usualmente dispuestos entre las hileras de estomas y la zona costal, de barba más larga que la base. *Papilas*: ausentes. *Macropelos*: presentes o ausentes, cuando presentes unicelulares, distribuidos en la región central de la zona intercostal o en los már-

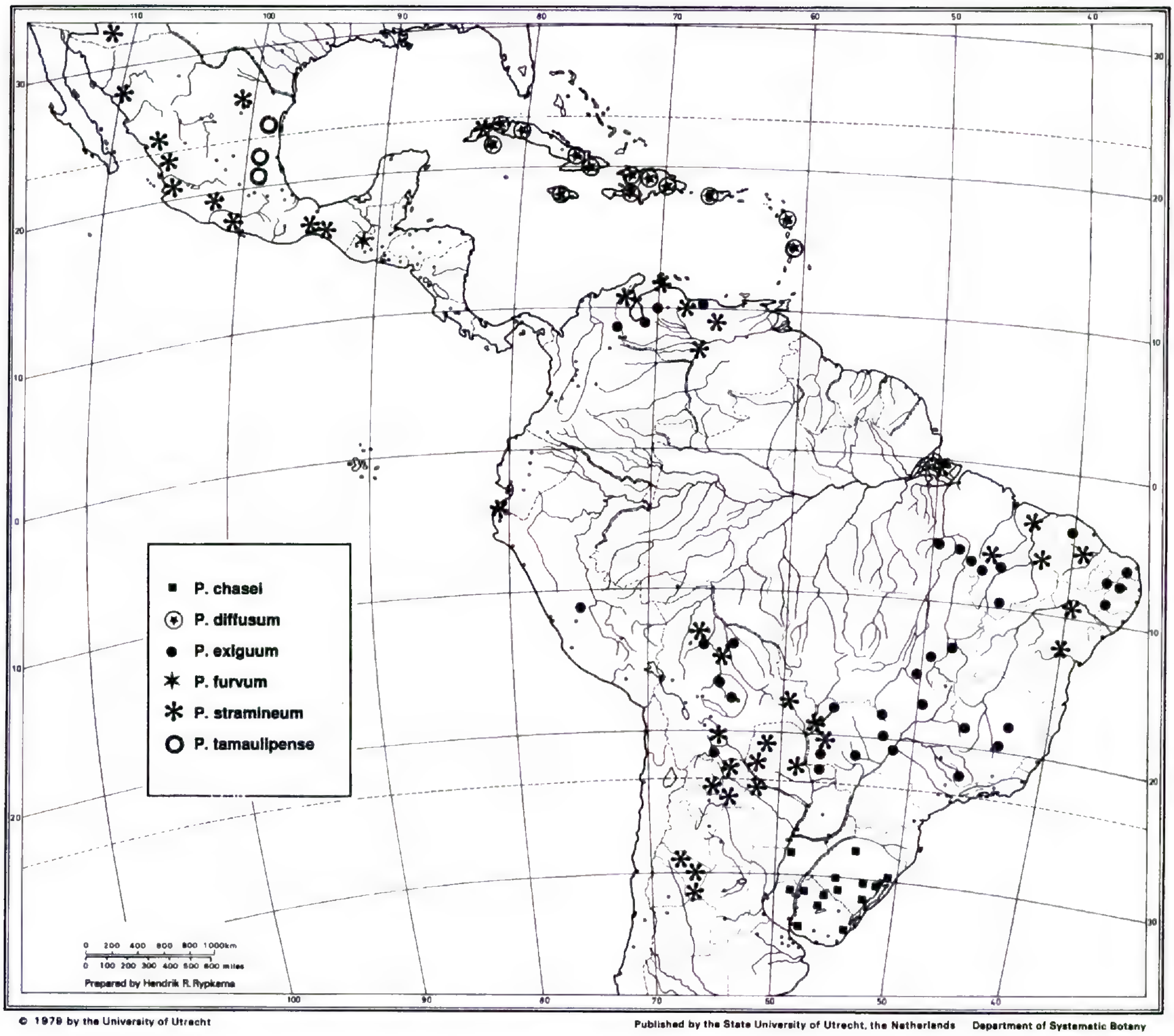


Figura 9. Distribución de *Panicum chasei, P. diffusum, P. exiguum, P. furvum, P. stramineum* y *P. tamaulipense.*

genes, variable en estructura: (a) de paredes delgadas, de 150–300 μm de largo, asociados a 2–4 células epidérmicas o (b) de 500–3350 μm de largo, rígidos, de paredes engrosadas, asociados a numerosas células epidérmicas sobreelevadas en relación al resto de la epidermis. *Cuerpos de sílice costales*: halteriformes, de eje longitudinal corto, menos frecuentemente nodulares, cruciformes o halteriformes de eje longitudinal alargado, distribuidos en 1–4 hileras longitudinales, alternando con células cortas; *cuerpos de sílice intercostales* usualmente cruciformes, menos frecuentemente de contorno irregular, homogéneamente distribuidos en la zona intercostal.

Epidermis adaxial en vista paradermal. Zonación: zonas costales e intercostales distinguibles; zonas intercostales heterogéneas, con una región central con células buliformes distinguibles de las laterales. *Células largas intercostales*: rectangulares, las centrales de paredes anticlinales delgadas y suavemente onduladas, las laterales con paredes suavemente engrosadas, las anticlinales longitudinales onduladas. *Células cortas intercostales*: solitarias o en pares sílico-suberosos, distribuidas en bandas a cada lado de las zonas costales, rectangulares o de contorno irregular, transversalmente alargadas. *Aparatos estomáticos*: similares a los presentes en la cara abaxial, distribuidos en 2 hileras en la zona intercostal. *Micropelos*: bicelulares, de estructura similar a los de la cara abaxial, presentes entre la banda estomática y la zona costal. *Aguijones*: frecuentes, raramente ausentes, distribuidos en hileras longitudinales en la zona costal. *Ganchos*: frecuentes en hileras longitudinales a ambos lados de la zona costal y las bandas estomáticas, menos frecuentemente aislados o ausentes. *Papilas*: ausentes, sólo presentes en ejemplares aislados de *P. stramineum* (*Allem 1479, Harley et al. 16294*),

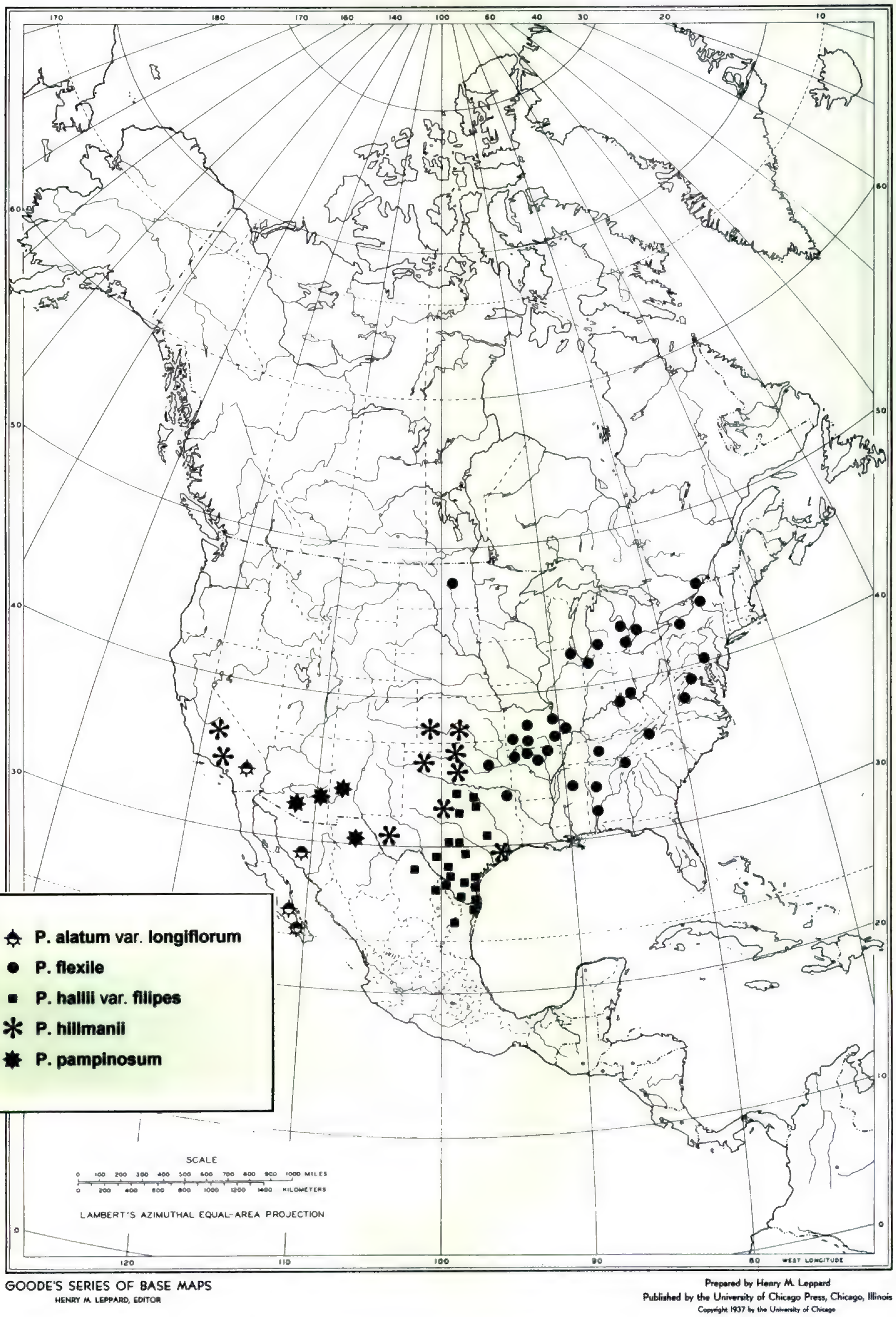


Figura 10. Distribución de *Panicum alatum* var. *longiflorum*, *P. hallii* var. *filipes*, *P. flexile*, *P. hillmanii* y *P. pampinosum*.

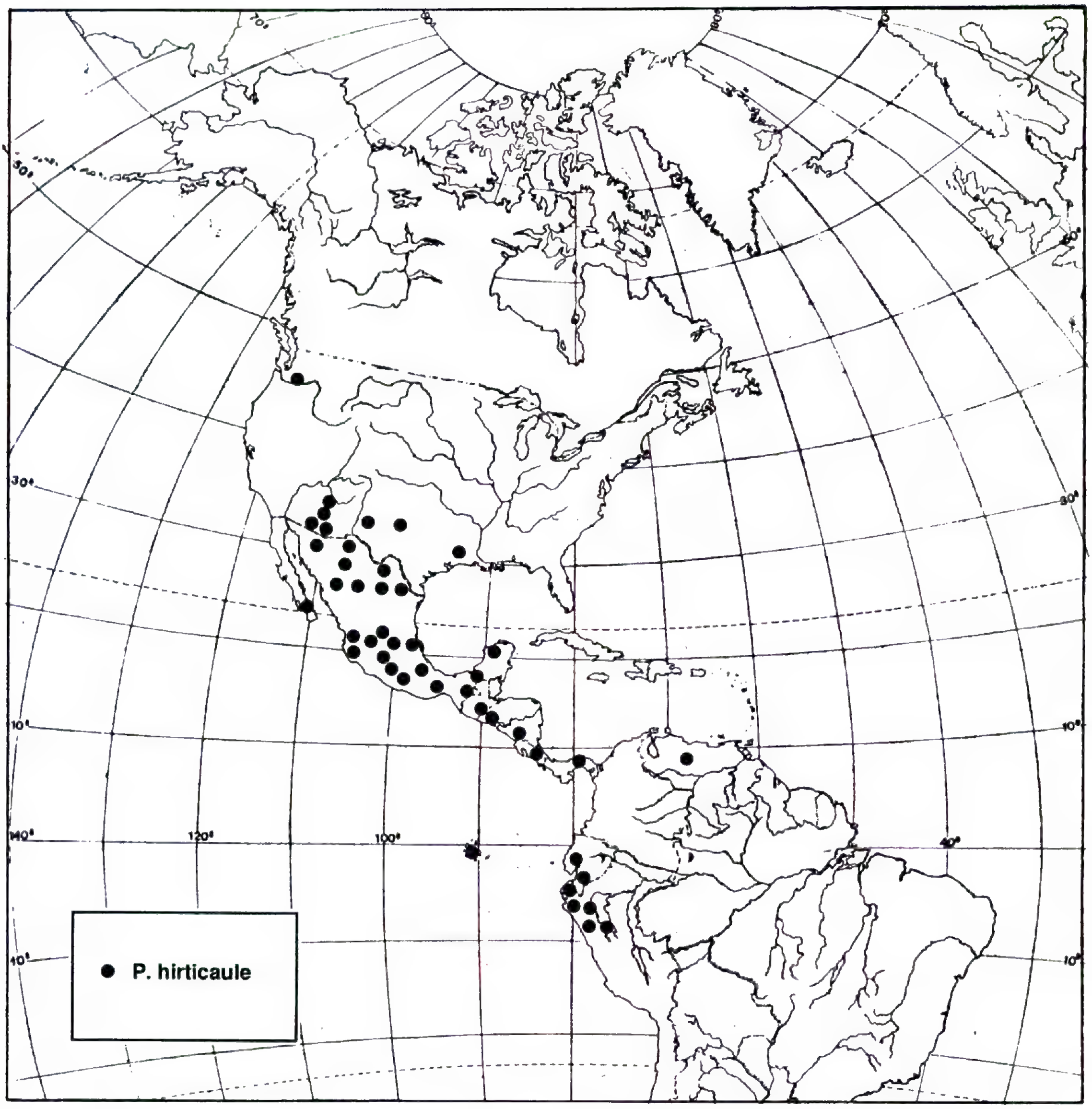


Figura 11. Distribución de *Panicum hirticaule*.

con 1–7 papilas por célula larga, distribuidas en hileras longitudinales, de diámetro mayor que ½ del ancho de la célula larga. *Macropelos* de frecuencia y estructura similar a los presentes en la cara abaxial. *Cuerpos de sílice costales*: halteriformes o a veces cruciformes, raramente nodulares; *cuerpos de sílice intercostales*: cruciformes o de contorno irregular, con su eje mayor transversalmente alargado, distribuidos entre las bandas estomáticas y la zona costal.

Las especies americanas de la sección *Panicum* poseen una anatomía foliar variable. Las hojas son planas, expandidas o en forma de "U" o "V," simétricas a ambos lados del nervio medio, incluyendo un número variable de haces vasculares desde 16–120 haces vasculares en transcorte. Las costillas y surcos presentan diferentes grados de desarrollo, desde poco manifiestos hasta ⅓ del ancho del transcorte, o con surcos adaxiales profundos, hasta ½ del ancho, como se observó en *P. aquarum*, *P. aztecanum* y *P. ephemeroides*. El nervio medio es también variable, con un haz vascular de primer orden estructuralmente indistinguible de los restantes laterales o estructuralmente distinguible, incluyendo 1–3 haces vasculares de primer orden y 2–5 haces vasculares de segundo orden, asociados o no a células parenquimáticas incoloras. Este rango de variación se observó dentro de una misma especie, como por ejemplo en *P. bergii*, *P. chasei*, *P. diffusum*, *P. ghiesbreghtii* y *P. stramineum*.

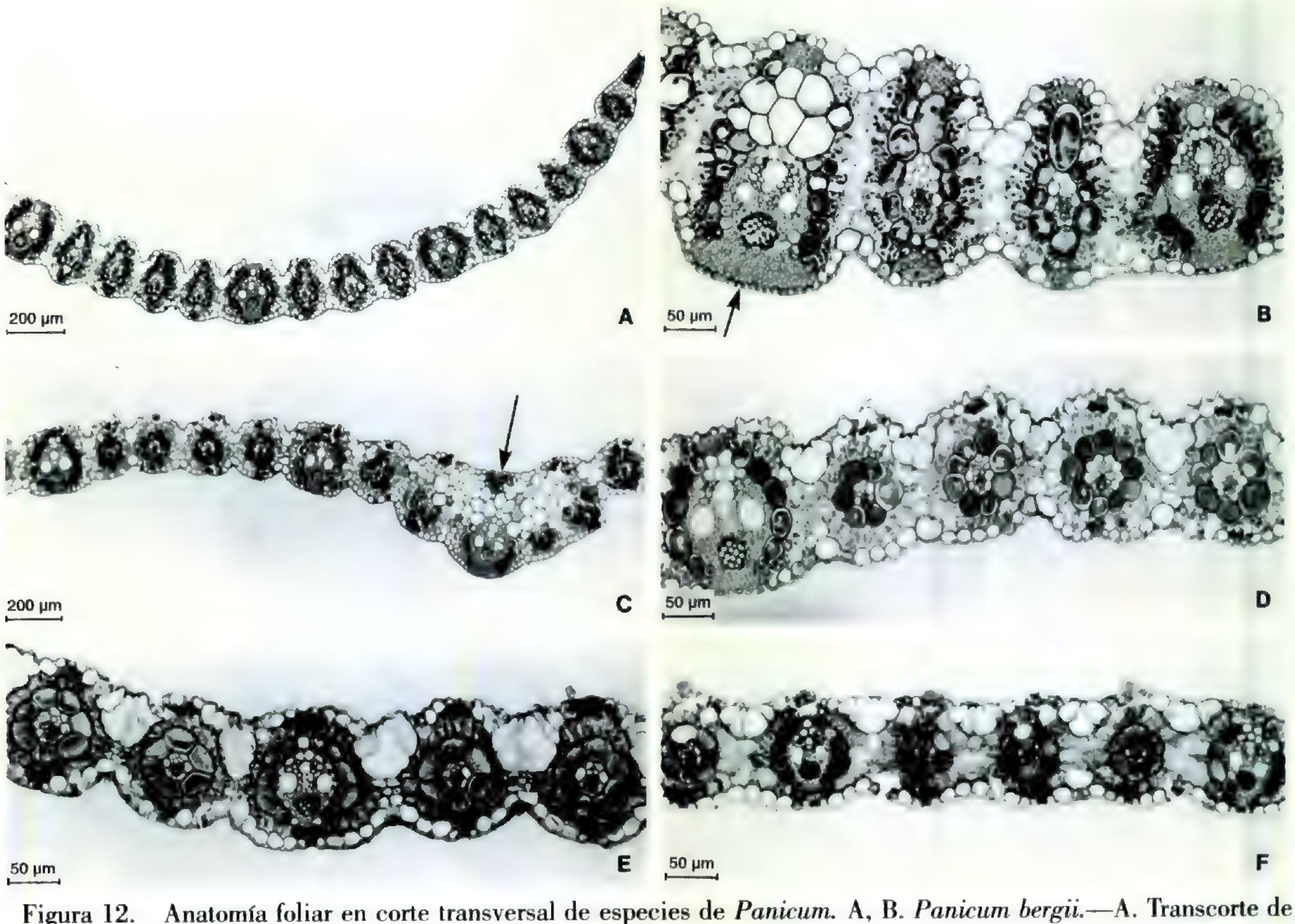


Figura 12. Anatomía foliar en corte transversal de especies de *Panicum*. A, B. *Panicum bergii*.—A. Transcorte de una porción de la lámina.—B. Detalle de la lámina, con haces vasculares de primer y segundo orden y células Kranz con cloroplastos marcadamente centrífugos, flecha señalando nervio medio. C, D. *Panicum stramineum*.—C. Transcorte de una porción de la lámina, flecha señalando nervio medio.—D. Detalle de la lámina con haces vasculares de primer y segundo orden y células Kranz con cloroplastos centrífugos.—E. *Panicum hispidifolium*, detalle de una porción de lámina, con haces vasculares de primer y segundo orden y células Kranz con cloroplastos centrípetos.—F. *Panicum peladoense*, detalle de una porción de lámina con haces vasculares de primer y segundo orden y células Kranz con cloroplastos centrípetos. (A, B, *Zuloaga et al. 2323*; C, D, *Zuloaga et al. 2515*; E, *Davidse & Pilz 31533*; F, *Zuloaga & Deginani 3447*.)

El mesófilo es conspicuamente radiado, compacto, continuo o interrumpido por trabas de esclerénquima, pudiéndose hallar columnas 1–3-seriadas de células parenquimáticas incoloras en contacto con ambas epidermis (en *P. alatum, P. aquarum, P. capillare, P. decolorans, P. hirsutum, P. hirticaule, P. hispidifolium, P. lepidulum, P. magnispicula, P. parcum* y *P. tamaulipense*) o sólo en contacto con las células buliformes (en *P. furvum*).

La presencia de una doble vaina alrededor de los haces vasculares, la externa con cloroplastos especializados, y por poseer mesófilo radiado, con 2(–3) células clorenquimáticas entre haces vasculares contíguos, nos permiten inferir que las especies de la sección *Panicum* son Kranz, del subtipo anatómico PS (= XYMS+), de acuerdo con los caracteres establecidos por Brown (1977), Ellis (1977) y Hattersley & Watson (1976).

La estructura de la vaina parenquimática de los haces vasculares presenta variaciones anatómicas, lo que permite distinguir dos grupos marcadamente diferenciados:

(A) con vainas de contorno regular, con células Kranz de paredes radiales y tangencial interna rectas, con cloroplastos alargados, de posición centrípeta. Dentro del mismo se incluyen a *P. alatum, P. aquarum, P. aztecanum, P. ephemeroides, P. exiguum, P. filipes, P. flexile, P. furvum, P. hallii, P. hillmanii, P. hispidifolium* (Fig. 12E), *P. hirticaule, P. magnispicula, P. miliaceum, P. mohavense, P. pampinosum, P. parcum, P. peladoense* (Fig. 12F), *P. philadelphicum, P. quadriglume* y *P. tamaulipense.*

(B) con vainas parenquimáticas de contorno irregular, con células Kranz de paredes radiales y tangencial externa arqueadas, con cloroplastos discoides, distribuidos centrifugamente. Se incluyen en este grupo a *P. bergii* (Fig. 12A, B), *P. capillare, P. capillarioides, P. chasei, P. decolorans, P. diffusum,*

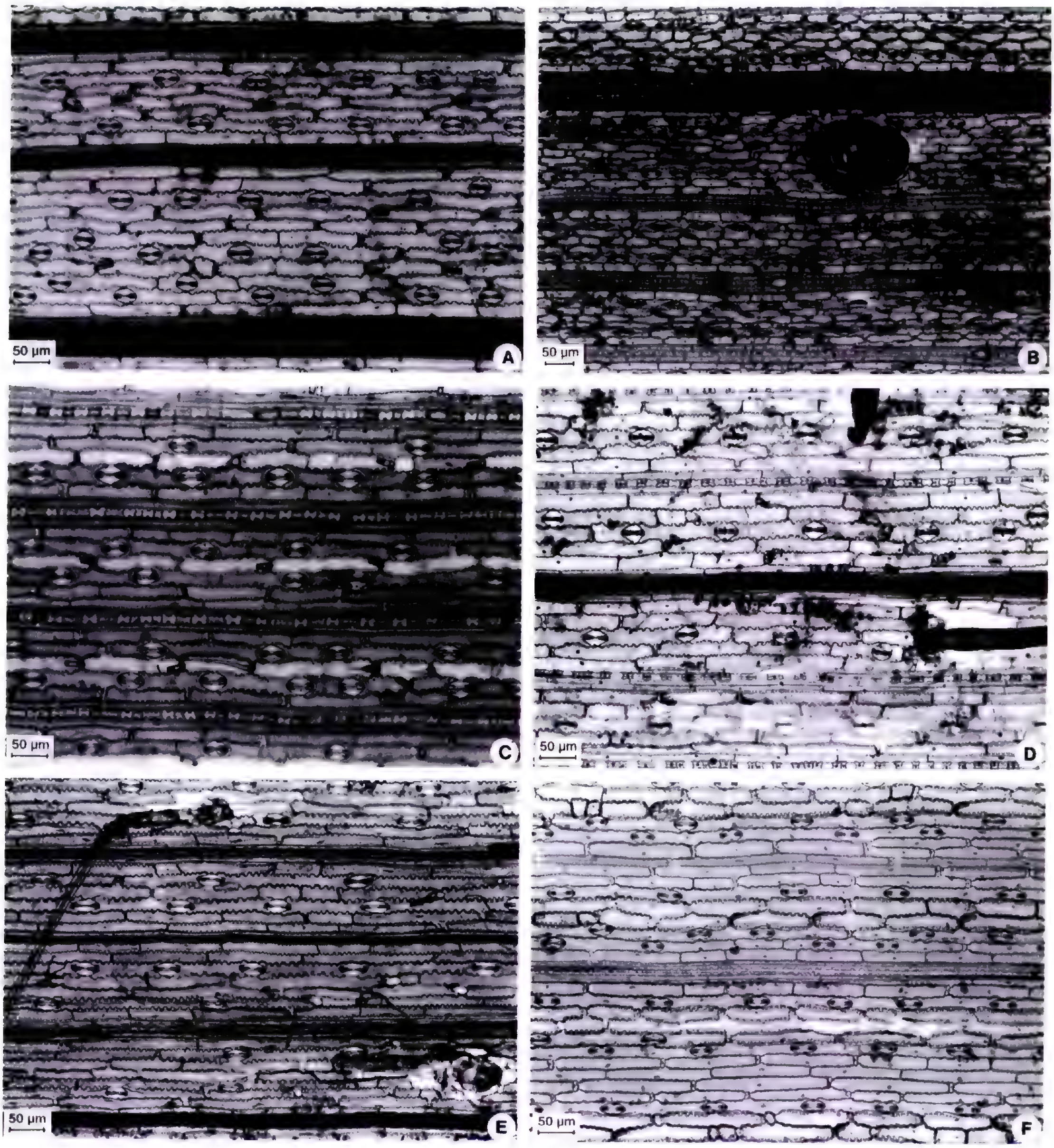


Figura 13. Epidermis abaxial de especies de *Panicum*.—A. *Panicum bergii*.—B. *Panicum capillare*.—C. *Panicum chasei*.—D. *Panicum peladoense*.—E. *Panicum quadriglume*.—F. *Panicum stramineum*. (A, *Zuloaga et al. 3072*; B, *Zuloaga & Morrone 3060*; C, *Cabrera & Zuloaga 32423*; D, *Zuloaga & Deginani 3447*; E, *Chase 8897*; F, *Zuloaga et al. 2515*.)

P. ghiesbreghtii, *P. hirsutum*, *P. lepidulum*, *P. mucronulatum* y *P. stramineum* (Fig. 12C, D).

Las especies del grupo A poseen cloroplastos centrípetos, característicos de las especies del subtipo anatómico NAD y fisiológico NAD-me (Gutiérrez et al., 1974). Las del grupo B tienen cloroplastos de posición centrífuga, estructura típica del subtipo anatómico PCK y que tradicionalmente ha sido asociada al tipo fisiológico PEP-ck (Gutiérrez et al., 1976). No obstante, la correlación estructural y funcional debe tomarse con precaución, dadas las excepciones halladas hasta el presente dentro de *Panicum*. Así, diversos autores citaron especies de *Panicum* con anatomía PCK y subtipo fotosintético NAD-me (Ohsugi & Murata, 1980; Ohsugi et al., 1982, Oguro et al., 1985, Prendergast et al., 1987). Dentro de la sección *Panicum*, *P. bergii* y *P. capillare*, especies que se incluyen en el grupo B y que corresponden al subtipo anatómico PCK, han sido descritas fisiológicamente como del tipo NAD-me (Gutiérrez et al., 1974; Prendergast et al., 1987).

Las similitudes exomorfológicas de los dos grupos anatómicos con cloroplastos centrípetos y centrífugos requieren inmediata confirmación del tipo fotosintético a través de estudios fisiológicos.

La distribución en América de las especies de la sección *Panicum* con anatomía NAD y PCK en relación a las divisiones políticas, muestra una marcada frecuencia relativa de especies NAD en América del Norte, con un 66%, 80% y 60% de especies NAD en Canadá, Estados Unidos de América y México respectivamente. Cabe destacar que México presenta la mayor concentración de especies de la sección, representada por el 48% de las mismas y un 10% de especies endémicas. A su vez, en las Islas del Caribe sólo se ha registrado la presencia de especies del tipo anatómico PCK. En América Central la relación entre las especies NAD y PCK es variable, predominando las especies NAD en una frecuencia del 60–75%, excepto en Belize y Costa Rica donde sólo se han registrado especies PCK. En América del Sur la frecuencia de especies NAD es relativamente baja, oscilando entre el 54 y el 66%, con una alta frecuencia relativa del 100% de especies PCK en Uruguay. Cabe destacar que en Brasil habita el 36% de las especies de la sección, con un 10% de especies endémicas. El patrón de distribución de los dos tipos anatómicos no muestra una clara predominancia de alguno de ellos en América; sin embargo serían necesario estudios más detallados de las relaciones fitogeográficas con los diferentes tipos anatómicos NAD y PCK. En lo que se refiere a la comparación entre los caracteres exomorfológicos e histofoliares, el estudio anatómico muestra marcadas diferencias entre especies exomorfológicamente afines. Así, *P. parcum*, especie que fue considerada como sinónimo de *P. decolorans* y que posee marcadas afinidades con *P. lepidulum*, pertenece anatómicamente al grupo A, o sea que es del subtipo anatómico NAD, mientras que *P. decolorans* y *P. lepidulum* poseen el subtipo anatómico PCK. *Panicum aztecanum*, especie de la que varios especímenes fueron previamente identificados como *P. lepidulum*, se distingue, además de diferencias exomorfólogicas que se discuten bajo esta especie, por tener un subtipo anatómico NAD. *Panicum diffusum*, especie erróneamente citada fuera de su área natural de Islas del Caribe por diferentes autores, se separa de *P. hallii* var. *filipes* por ser anatómicamente PCK. *Panicum hirticaule*, especie afín a *P. ghiesbreghtii* y *P. stramineum*, se caracteriza por tener anatomía NAD, mientras que los dos últimos taxones son PCK.

Algo similar ocurre con *P. mohavense* y *P. stramineum*, siendo la primera del subtipo anatómico NAD y la segunda del subtipo anatómico PCK. Finalmente, *P. capillare* se distingue por ser anatómicamente una especie PCK, mientras que *P. flexile*, *P. hillmanii* y *P. philadelphicum*, especies afines de América del Norte, son uniformemente del subtipo anatómico NAD.

Discusión

Las especies de la sección *Panicum* poseen caracteres anatómicos y exomorfológicos diagnósticos del subgénero *Panicum*. El subgénero se caracteriza por incluir especies Kranz, del subtipo anatómico PS (=XyMS+) (Hattersley & Watson, 1976; Brown, 1977), con 2 vainas alrededor de los haces vasculares, la interna mestomática y la externa Kranz, con cloroplastos especializados, mesófilo compacto, radiado, y con 2–3 células clorenquimáticas entre haces vasculares. Además este subgénero posee un número básico de cromosomas $x = 9$ e incluye especies con espiguillas elipsoides a largamente ovoides, con gluma inferior de tamaño variable y gluma superior y lemma inferior comúnmente 7–9-nervias (excepcionalmente 5-nervias en algunas especies y hasta 13–15-nervias en otros taxones). El antecio superior es uniforme en el subgénero, crustáceo, liso, con papilas simples o con papilas verrugosas en el ápice de la pálea, menos frecuentes en toda superficie (Zuloaga, 1987a).

Las especies del subgénero *Panicum* habitan usualmente ambientes abiertos y secos, a excepción de especies de *Dichotomiflora*, las que crecen en bordes de ríos.

Hitchcock & Chase (1910) consideran informalmente a las especies americanas de la sección *Panicum* dentro de los grupos Capillaria y Diffusa, tomando en cuenta si las especies son anuales o perennes respectivamente. Pohl (1980), McVaugh (1983) y Zuloaga (1987a) consideran que este carácter no resulta diagnóstico para distinguir a las especies aquí agrupadas en la sección *Panicum*, resultando el mismo de difícil distinción en regiones tropicales (McVaugh, 1983). A la vez las especies consideradas aquí en la sección *Panicum* poseen una combinación de caracteres diagnósticos comunes: la misma incluye plantas cespitosas, con cañas usualmente simples o ramificadas en la base (excepcionalmente ramificadas en los nudos superiores en *P. aquarum*); las lígulas son membranáceo-ciliadas y las láminas oblongo-lanceoladas a filiformes. Las inflorescencias son piramidales, laxas y difusas, raramente con las ramas adpresas, con espiguillas ovoides a largamente elipsoides, divergentes o más o menos adpresas, dispuestas no unilateralmente. El largo de la gluma inferior es vari-

able, comúmente de ½ a ¾. La gluma superior y lemma inferior son 7–9-nervias y superan en largo al antecio superior. La pálea inferior alcanza igual largo que la lemma inferior o está reducida a ausente en algunas especies; la flor inferior es ausente. Finalmente el antecio superior es crustáceo y brillante y siempre lleva papilas hacia el ápice de la pálea superior.

Diversas modificaciones estructurales, presentes en las espiguillas e inflorescencias de las especies de la sección *Panicum,* sugieren diversos mecanismos de dispersión. En primer lugar la presencia de lemma y pálea endurecidas encerrando a la cariopsis a la madurez fue correlacionada a la dispersión por animales granívoros o herbívoros, los que ingieren las diásporas accidental o intencionalmente (Ridley, 1930; van der Pijl, 1982). Thomasson (1985) sugiere que las brácteas endurecidas protegen a la cariopsis del ataque de insectos o durante el pasaje de la misma a través del tracto digestivo de los animales.

Dentro de la sección *Panicum* se ha observado, a diferencia de lo que ocurre en el resto del género, que el antecio superior es tempranamente caedizo. Este mecanismo de dispersión está correlacionado, en *Panicum exiguum, P. furvum, P. peladoense* y *P. quadriglume,* con el hecho de que al madurar la cariopsis la gluma superior cae, dejando el dorso del antecio superior al descubierto, siendo este último de color negro y brillante. Un síndrome semejante al hallado en las especies americanas descritas, fue observado en *P. atrosanguineum* A. Rich., especie que habita en Africa y en el NW de la India (Clayton, 1989). Van der Pijl (1982) indica que la presencia de color llamativo y rigidez a la madurez en las diásporas funcionaría como un mecanismo de atracción para las aves granívoras.

Adicionalmente a la caída prematura del antecio superior, en *Panicum bergii* y *P. capillare* las inflorescencias desarticulan en su conjunto a la madurez y son dispersadas por el viento.

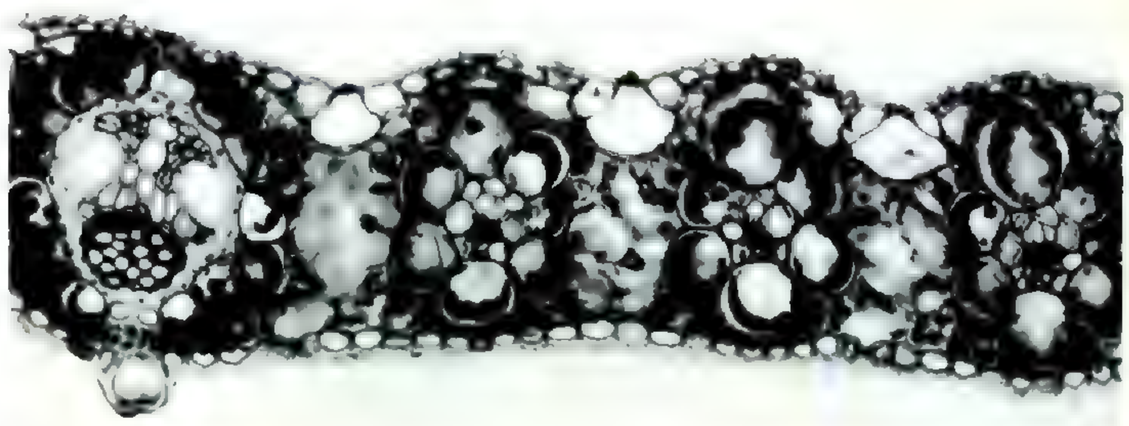
Finalmente, la presencia en *Panicum alatum* de eleosomas en la base de la lemma permite sugerir que las diásporas en esta especie se dispersan a través de hormigas. Beattie (1983) sugiere diversos significados adaptativos para el establecimiento de la mirmecofilia, entre las que se incluyen protección al fuego, dispersión a distancia y el hecho de poseer los hormigueros un microhabitat rico en nutrientes. Apéndices aliformes similares a los presentes en *Panicum alatum* en los márgenes basales de la lemma, han sido señalados en especies de *Ichnanthus* y *Echinolaena* (Davidse, 1987).

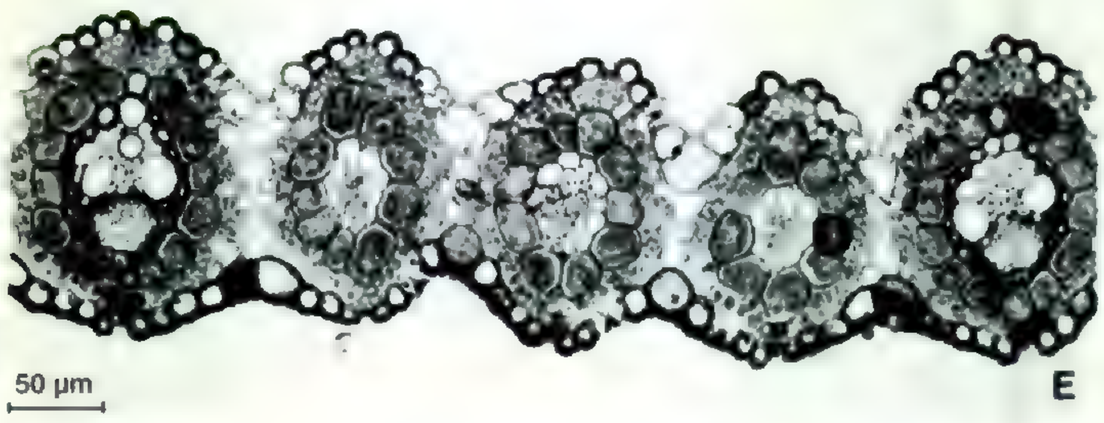
RELACIÓN CON SECCIONES DEL SUBGÉNERO *PANICUM*

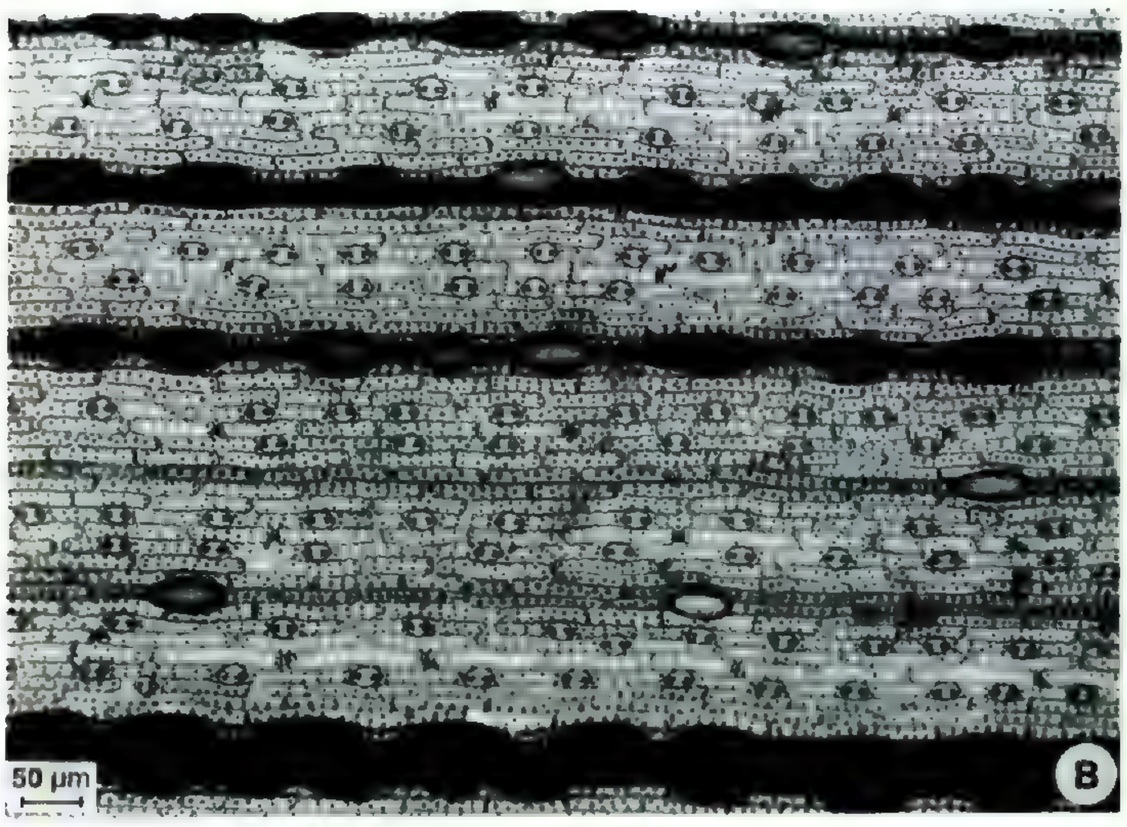
La sección típica se relaciona en América, dentro del subgénero *Panicum,* con las secciones *Rudgeana, Virgata* Hitchc. & Chase, *Urvilleana* (Hitchc. & Chase) Pilg. y *Dichotomiflora* (Hitchc. & Chase) Honda. La sección *Rudgeana* es exclusivamente americana y comprende 5 especies distribuidas desde Mesoamérica y las Islas del Caribe hasta Bolivia y Brasil. Esta sección es, desde el punto de vista anatómico, exclusivamente del subtipo NAD (Fig. 14C, D) y se distingue de las especies de la sección *Panicum* que poseen este subtipo anatómico por incluir taxones con espiguillas marcadamente abiertas a la madurez y de inserción oblícua, con gluma inferior acuminada a subulada y antecio superior separado por un conspicuo entrenudo de la raquilla. El entrenudo es dorsiventralmente comprimido y heterogéneo, constituído por dos porciones, una porción basal y dorsal rígida, lisa y brillante, de la misma consistencia que el antecio superior, y una porción ventral junto a la pálea del antecio superior constituída por tejido membranáceo (Zuloaga, 1987b).

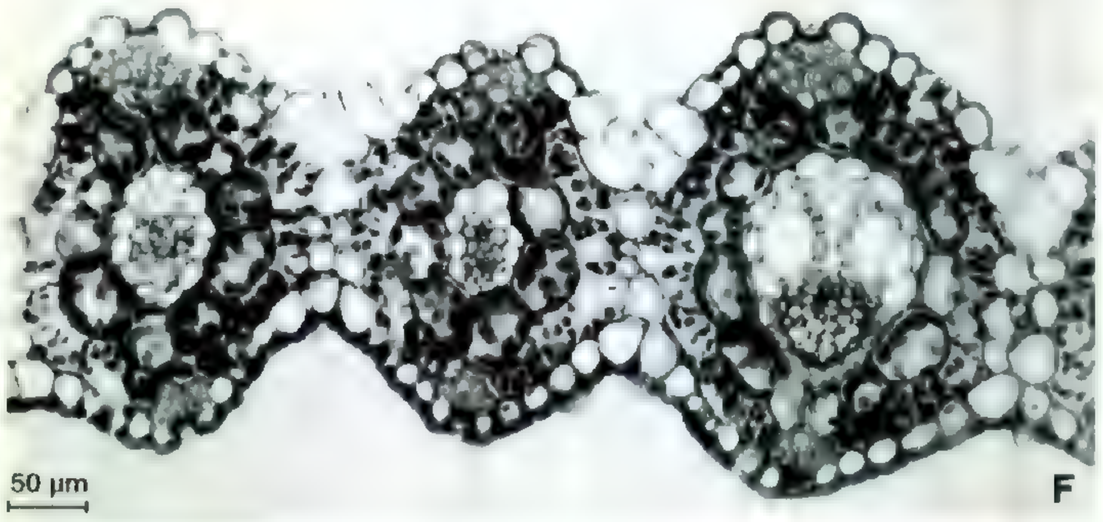
Las especies PCK de la sección *Panicum* poseen una anatomía similar a las especies de *Dichotomiflora*; esta última se caracteriza por tener además papilas simples en la epidermis adaxial o en ambas (Fig. 14A, B) (Ellis, 1988; Zuloaga et al., 1993). Papilas adaxiales fueron halladas en especímenes aislados de *P. stramineum.* Las especies de la sección *Dichotomiflora* crecen en lugares húmedos, siendo frecuentes en bordes de ríos, con cañas erectas a decumbentes, arraigadas en los nudos inferiores. Las espiguillas en esta sección poseen gluma inferior 1–3-nervia, ⅙ a ¼(–½) del largo de la gluma superior y la lemma inferior.

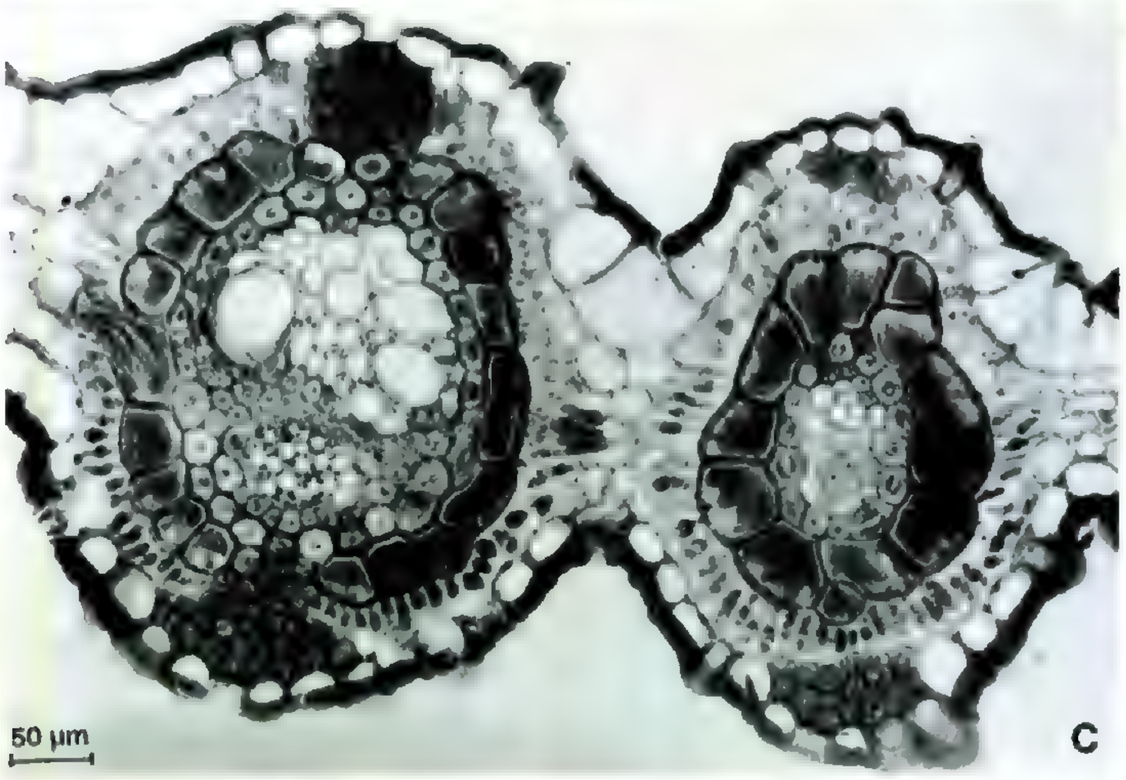
Las secciones *Urvilleana* y *Virgata* difieren de las especies de la sección *Panicum* por tener cloroplastos discoides, distribuidos periféricamente en las células Kranz (Fig. 14E–H) (Zuloaga et al., 1993). Las especies de *Urvilleana* se distinguen anatómicamente por tener haces vasculares de primer, segundo y tercer orden, estos últimos distribuidos por debajo de las células buliformes, con extensiones adaxiales de la vaina desarrolladas en los haces vasculares de primer y segundo orden, y surcos profundos; más de ½ del ancho del transcorte. Exomorfológicamente *Urvilleana* se distingue por incluir especies que habitan en dunas o sobre suelos arenosos con rizomas cundidores, láminas involutas, rígidas, densamente pilosas, espiguillas pilosas con gluma inferior ¾ a ⅘ del largo de la espiguilla, flor inferior presente y antecio superior piloso hacia la base, con largos pelos blan-











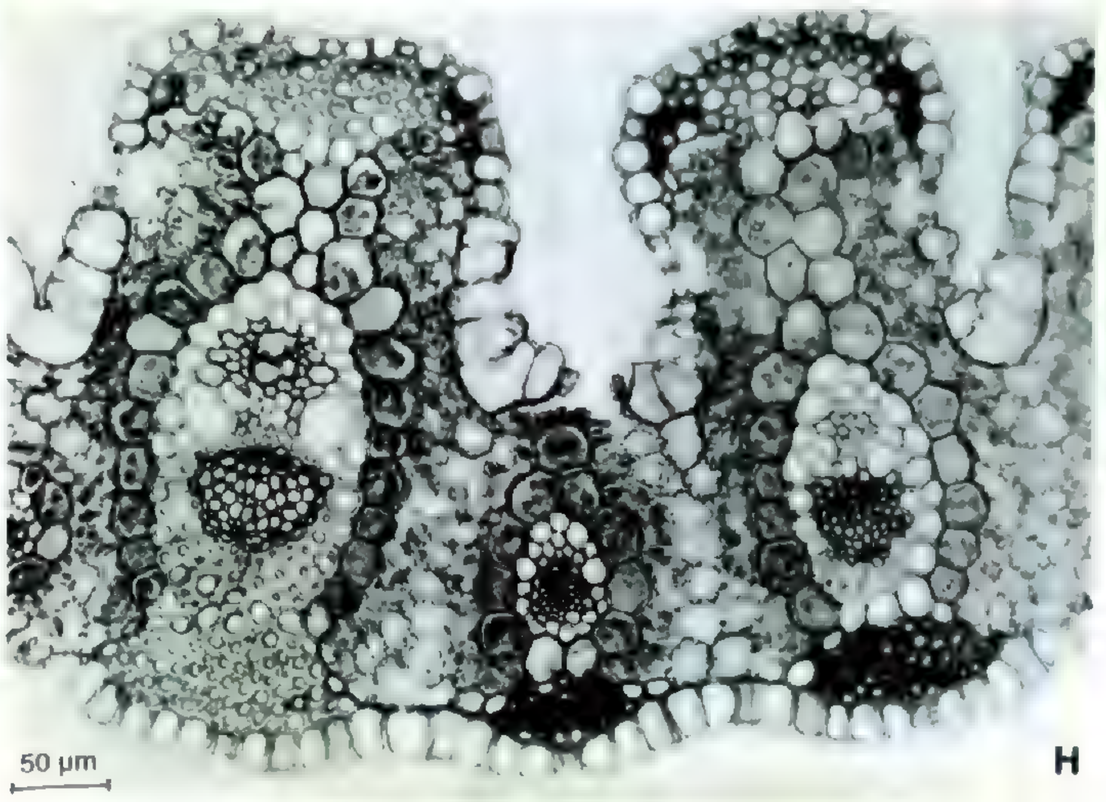


Figura 14. Anatomía foliar de especies de *Panicum*. A, B. *Panicum elephantipes*.—A. Detalle en transcorte de una porción de lámina, con haces vasculares de primer y segundo orden, células Kranz con cloroplastos centrífugos y papilas sobre ambas epidermis.—B. Epidermis abaxial, con papilas y aguijones costales.—C. *Panicum cervicatum*. Detalle en transcorte de una porción de la lámina con haces vasculares de primer y segundo orden y células Kranz con cloroplastos centrípetos.—D. *Panicum cayennense*. Detalle en transcorte de una porción de la lámina con haces vasculares de primer y segundo orden y células Kranz con cloroplastos centrípetos. E, F. *Panicum tricholaenoides*.—E. Transcorte de una porción de la lámina con haces vasculares de primer y segundo orden.—F. Células Kranz con cloroplastos de distribución marcadamente periférica. G, H. *Panicum racemosum*.—G. Detalle en transcorte de una porción de la lámina.—H. Transcorte con haces vasculares de primer, segundo y tercer orden, células Kranz con cloroplastos periféricos. (A, *Zuloaga 2338*; B, *Zuloaga 3084*; C, *Zuloaga 3837*; D, *Zuloaga 3978*; E, *Zuloaga s.n.*; F, *Zuloaga et al. 2304*; G, H, *Zuloaga 3360*.)

quecinos. Las especies de *Virgata* poseen asimismo rizomas cundidores, cañas rígidas, espiguillas con flor inferior presente.

Panicum maximum Jacq., especie del género perteneciente al subgénero *Megathyrsus* Pilg. y que anatómicamente se caracteriza por ser del subtipo PCK, difiere de las especies de la sección típica por ser una especie con gluma inferior reducida, por tener gluma superior y lemma inferior 5-nervias, flor inferior estaminada y antecio superior transversalmente rugoso (Zuloaga, 1987a).

RELACIÓN CON OTROS GÉNEROS DE LA TRIBU PANICEAE

La sección *Panicum* se separa, dentro de la tribu Paniceae, de géneros afines y con anatomía PCK por las siguientes características: *Urochloa* posee ramificaciones de la inflorescencia racemosas y antecio superior transversalmente rugoso, mucronado a crestado, no caedizo; *Brachiaria* posee ramificaciones de la inflorescencia con espiguillas dispuestas unilateralmente, espiguillas vilosas con gluma inferior $\frac{1}{5}$ o menos del largo de la espiguilla y antecio superior completamente liso, sin papilas; *Eriochloa* posee una dilatación cupuliforme en la base de la espiguilla, con la gluma inferior fusionada a dicha dilatación, y antecio superior transversalmente rugoso. Cabe destacar que además estos géneros son desde el punto de vista fisiológico PEP-ck.

Dentro de los géneros NAD de la tribu Paniceae, *Panicum* se separa de *Scutachne* Hitchc. & Chase, género endémico de las Antillas, por tener este último gluma superior y lemma inferior coriáceas, y de *Yakirra* y *Arthragrostis* Lazarides, géneros endémicos de Australia, por incluir el primero especies con un conspicuo entrenudo en la base del antecio superior y el último por poseer articulaciones en la base de ramificaciones de la inflorescencia, pedicelos y espiguillas.

Tratamiento Taxonómico

Panicum L. secc. **Panicum**. ESPECIE TIPO: *Panicum miliaceum* Linnaeus (lectótipo, designado por Hitchcock & Chase, 1910).

P. secc. *Miliaceae* Stapf in Prain, Fl. Trop. Afr. 9: 640. 1920.

Plantas anuales o perennes, cespitosas a arrosetadas y con *cañas* erectas a ocasionalmente decumbentes, simples a ramificadas; entrenudos huecos. *Vainas* sin aerénquima, excepto en *P. aquarum*. *Lígulas* membranáceo-ciliadas. *Láminas* oblongo-lanceoladas a filiformes, planas o con los bordes involutos. *Inflorescencias* terminales y axilares, laxas y difusas con ramificaciones divergentes del raquis, a espiciformes o subespiciformes, con ramificaciones adpresas al eje principal. *Espiguillas* globosas u ovoides a largamente elipsoides, solitarias, no estipitadas a estipitadas, glabras. *Gluma inferior* $(\frac{1}{3}–)\frac{1}{2}–\frac{3}{4}(–\frac{4}{5})$ del largo de la espiguilla, 3–5(7–9)-nervia. *Gluma superior* y *lemma inferior* subiguales, de igual largo o superando en longitud al antecio superior, (5–)7–9(–15)-nervias; gluma superior tempranamente caediza (en *P. exiguum*, *P. furvum*, *P. peladoense* y *P. quadriglume*). *Pálea inferior* presente, de igual largo o mayor que el antecio superior, a reducida o ausente; flor inferior ausente. *Antecio superior* crustáceo, liso a papiloso en toda su superficie, glabro, brillante a opaco, pajizo, grisáceo o castaño a negro a la madurez, cayendo desnudo a la madurez sin las restantes brácteas; lemma envolviendo con sus bordes a la pálea, esta 2-nervia con papilas verrugosas o simples hacia el ápice; lodículas 2, truncadas, cuneiformes; estambres 3; estilos 2, estigmas plumosos. *Cariopsis* con hilo punctiforme a oblongo; embrión $\frac{1}{3}–\frac{1}{2}$ del largo de la cariopsis, ocasionalmente mayor.

Plantas C_4, del subtipo fisiológico NAD-me.
Número básico de cromosomas $x = 9$.

Sección con 31 especies en América, distribuidas desde Canadá hasta la República Argentina. Habitan en campos, en lugares secos.

Clave de las Especies

1. Antecio superior negro a la madurez; gluma superior caediza a la madurez, dejando al descubierto el antecio 2
1. Antecio superior pajizo a castaño a la madurez; gluma superior no caediza a la madurez 5

2(1). Espiguilla triflora, con una flor inferior estéril, una intermedia estaminada y una flor superior perfecta; antecio superior con el dorso de la lemma hacia la gluma inferior ..... 29. *P. quadriglume*

2. Espiguilla biflora, con una flor inferior estéril y una flor superior perfecta; antecio superior con el dorso de la lemma hacia la gluma superior 3

3(2). Plantas anuales; gluma inferior $\frac{3}{4}–\frac{4}{5}$ del largo de la espiguilla ..... 11. *P. exiguum*

3. Plantas perennes; gluma inferior $\frac{1}{2}–\frac{3}{4}$ del largo de la espiguilla 4

4(3). Plantas de 16–20 cm de alto; inflorescencias de 3–6 cm de largo; espiguillas de 2.4–2.7 mm de largo; Guatemala ..... 13. *P. furvum*

4. Plantas de 20–60 cm de alto; inflorescencias de 7–22 cm de largo; espiguillas de (2.5–)2.7–3.3(–3.7) mm de largo; América del Sur, en Bolivia, Brasil, Paraguay, Uruguay y la Argentina ..... 27. *P. peladoense*

5(1). Plantas de ambientes acuáticos, vainas con aerénquima; cañas manifiestamente ramificadas en los nudos superiores ..... 2. *P. aquarum*

5. Plantas de ambientes secos a moderadamente

húmedos, vainas sin aerénquima; cañas simples a profusamente ramificadas en los nudos medios y/o basales 6
6(5). Inflorescencias espiciformes a subespiciformes, con ramificaciones de primer orden adpresas al eje principal 7
6. Inflorescencias laxas, difusas a contraidas, con ramificaciones de primer orden divergentes del eje principal 11
7(6). Espiguillas de 2–4 mm de largo; antecio superior con dos cicatrices basales 8
7. Espiguillas de (4.2–)5–6 mm de largo; antecio superior con un anillo circular en la base 10
8(7). Espiguillas de 2–2.2 mm de largo; plantas de 2–6(–8) cm de alto, arrosetadas, con inflorescencias subincluidas en las vainas foliares ..... 23. *P. mohavense*
8. Espiguillas de 2.8–4 mm de largo; plantas de 11–80 cm de alto, no arrosetadas, con inflorescencias largamente exertas 9
9(8). Espiguillas globosas; gluma inferior $\frac{4}{5}$ del largo de la espiguilla; pálea inferior reducida, $\frac{1}{3}$ del largo del antecio superior; inflorescencias de 5–6 cm de largo; plantas anuales; Estados Unidos de América y México ..... 25. *P. pampinosum*
9. Espiguillas anchamente ovoides; gluma inferior $\frac{1}{2}$–$\frac{3}{4}$ del largo de la espiguilla; pálea inferior tan larga como el antecio superior; inflorescencias de 8–24 cm de largo; plantas perennes; sur de Brasil a la Argentina ..... 7. *P. chasei*
10(7). Inflorescencias paucifloras de 3–6 cm de largo; gluma inferior $\frac{3}{4}$ o más del largo de la espiguilla, separada de la gluma superior por un entrenudo conspicuo; Brasil ..... 21. *P. magnispicula*
10. Inflorescencias multifloras de (5–)10–20 cm de largo; gluma inferior $\frac{1}{2}$ o menos del largo de la espiguilla, sin un entrenudo marcado entre la gluma inferior y superior; México. ..... 8. *P. decolorans*
11(6). Inflorescencias caedizas en conjunto a la madurez por ruptura del pedúnculo 12
11. Inflorescencias no caedizas 14
12(11). Plantas anuales; pálea inferior ausente a vestigial, hasta de 0.3 mm de largo 5. *P. capillare*
12. Plantas perennes; pálea inferior elíptica, de aproximadamente igual largo que el antecio superior 13
13(12). Raquis y ramificaciones de la inflorescencia glabros; vainas y láminas esparcidamente pilosas a glabrescentes .... 4a. *P. bergii* var. *bergii*
13. Raquis y ramificaciones de la inflorescencia, vainas y láminas densamente híspidas ..... 4b. *P. bergii* var. *pilosissimum*
14(11). Plantas robustas hasta de 3 m de alto; vainas con pelos urticantes ..... 17. *P. hirsutum*
14. Plantas menores hasta de 1.50 m de alto; vainas glabras a hirsutas pero sin pelos urticantes 15
15(14). Plantas perennes 16
15. Plantas anuales 24
16(15). Espiguillas de (3.3–)3.6–6.4 mm de largo ... 17
16. Espiguillas de 1.8–3.1 mm de largo 20
17(16). Espiguillas de 5–6.4 mm de largo; gluma superior y lemma inferior 3.2–4 mm más largas que el antecio superior ..... 6. *P. capillarioides*
17. Espiguillas de (3.3–)3.6–4.5 mm de largo; gluma superior y lemma inferior 0.8–1.5 mm más largas que el antecio superior 18
18(17). Plantas glaucas; láminas basales rizadas ..... 15a. *P. hallii* var. *hallii*
18. Plantas no glaucas, láminas basales no rizadas 19
19(18). Espiguilla con un estípite en la base; gluma inferior y superior separadas por un entrenudo de 0.5 mm del largo; gluma superior 7–9-nervia; láminas lineares a filiformes, de 0.1–0.3 cm de ancho ..... 3. *P. aztecanum*
19. Espiguilla sin un estípite en la base; gluma inferior y superior sin un entrenudo marcado; gluma superior 9–15-nervia; láminas linear-lanceoladas, de 0.4–1.2 cm de ancho ..... 20. *P. lepidulum*
20(16). Láminas no glaucas; láminas basales no rizadas; láminas densamente pilosas 21
20. Láminas glaucas; láminas basales ligera a marcadamente rizadas; láminas glabras a esparcidamente hirsutas 22
21(20). Plantas de 40–90(–120) cm de alto; cuello densamente piloso; hojas erectas, ascendentes ..... 14. *P. ghiesbreghtii*
21. Plantas de (6–)15–60 cm de alto; cuello glabro; hojas patentes ..... 9. *P. diffusum*
22(20). Espiguillas de 2.7–3.1 mm de largo; espiguillas adpresas sobre las ramas de la inflorescencia ..... 15a. *P. hallii* var. *hallii*
22. Espiguillas de 1.8–2.8 mm de largo; espiguillas difusas sobre las ramas de la inflorescencia 23
23(22). Espiguillas de 2.1–2.8 mm de largo; gluma superior y lemma inferior 0.3–0.7 mm más largas que el antecio superior; láminas de 11–23 cm de largo por 0.2–0.4 cm de ancho ..... 15b. *P. hallii* var. *filipes*
23. Espiguillas de 1.8–2.2 mm de largo; gluma superior y lemma inferior tan largas como el antecio superior; láminas de 20–35(–50) cm de largo por 0.5–0.8 cm de ancho ..... 31. *P. tamaulipense*
24(15). Antecio superior obovoide a la madurez, cortamente estipitado, con 2 expansiones carnosas en la base de la lemma 25
24. Antecio superior ovoide a elipsoide, no estipitado, sin expansiones basales, con 2 cicatrices basales o con un anillo en la base de la lemma 27
25(24). Espiguillas de 3.6–4.5 mm de largo ..... 1b. *P. alatum* var. *longiflorum*
25. Espiguillas de 2.4–3(–3.2) mm de largo 26
26(25). Antecio superior fuertemente papiloso en toda su superficie, opaco ..... 1a. *P. alatum* var. *alatum*
26. Antecio superior liso, brillante, con papilas hacia el ápice de la pálea ..... 1c. *P. alatum* var. *minus*
27(24). Espiguillas de 4.5–6 mm de largo 28
27. Espiguillas de 1.6–4 mm de largo 29
28(27). Espiguillas estipitadas, con un conspicuo entrenudo entre la gluma superior y lemma inferior; antecio superior tardíamente caedizo; panojas erectas ..... 26. *P. parcum*
28. Espiguillas no estipitadas, sin entrenudos de la raquilla consipcuamente marcados; ante-

cio superior tempranamente caedizo; panojas nutantes ..... 22. *P. miliaceum*

29(27). Panojas parcialmente incluidas en las hojas superiores, con las ramificaciones inferiores verticiladas; antecio superior con dos cicatrices basales conspicuas, ca. 0.6 mm de largo ..... 16. *P. hillmanii*

29. Panojas exertas, con ramificaciones inferiores opuestas o alternas; antecio superior con dos cicatrices basales, menores de 0.6 mm de largo o con un anillo en la base de la lemma 30

30(29) Pálea inferior desarrollada, ¾–1/1 del largo del antecio superior 31

30. Pálea inferior reducida, ½ o menos del largo del antecio superior o ausente 34

31(30). Láminas lineares, de 20–23 cm de largo, 0.2 cm de ancho; espiguillas adpresas en las ramas; lemma inferior 5-nervia; antecio superior con un anillo en la base de la lemma 10. *P. ephemeroides*

31. Láminas lanceoladas a linear-lanceoladas, de 4.5–45 cm de largo, 0.3–1.5(–2) cm de ancho; espiguillas difusas sobre las ramificaciones; lemma inferior 7–11-nervia; antecio superior con dos cicatrices en la base de la lemma o con un anillo en *P. hispidifolium*, con espiguillas globosas y pálea inferior ¾ del largo del antecio superior 32

32(31). Espiguillas ovoides; gluma superior y lemma inferior 1 mm más largas que el antecio superior; láminas lanceoladas 24. *P. mucronulatum*

32. Espiguillas globosas; gluma superior y lemma inferior tan largas como el antecio superior o hasta 0.4 mm más largas; láminas linear-lanceoladas 33

33(32). Gluma inferior ⅓–½ del largo de la espiguilla; gluma superior 9–11(–13)-nervia; pálea inferior igual o más larga que el antecio superior; espiguillas de 2.3–3.2 mm de largo ..... 30. *P. stramineum*

33. Gluma inferior ½–¾ del largo de la espiguilla; gluma superior 7-nervia; pálea inferior ¾ del largo del antecio superior; espiguillas de 3.2–3.7 mm de largo 19. *P. hispidifolium*

34(30). Gluma superior y lemma inferior tan largas como el antecio superior o hasta 0.3 mm más largas ..... 28. *P. philadelphicum*

34. Gluma superior y lemma inferior 0.8–1.6 mm más largas que el antecio superior 35

35(34). Pálea inferior ausente; gluma inferior ⅓–½ del largo de la espiguilla; antecio superior con un anillo en la base de la lemma ..... 12. *P. flexile*

35. Pálea inferior ⅓–½ del largo del antecio superior; gluma inferior ½–¾ del largo de la espiguilla; antecio superior con dos cicatrices en la base de la lemma, de ca. 0.2 mm de largo 36

36(35). Antecio superior conspicuamente papiloso, opaco ..... 18b. *P. hirticaule* var. *verrucosum*

36. Antecio superior liso, brillante, con papilas junto al ápice de la pálea 18a. *P. hirticaule* var. *hirticaule*

1. Panicum alatum Zuloaga & Morrone, sp. nov. TIPO: México. Baja California Sur: 15.5 mi. S of El Arco, 27°45′N, 113°20′W, 23 Oct. 1959, *Wiggins 15160**,** (holótipo, MO; isótipos, GH, LA, MEXU, SI). Figura 15.

Panico hirticauli affine sed lemma superiore base bialata et anthoecio superiori obovoideo et stipitato differt.

Plantas anuales, cespitosas, de 13–95 cm de alto. *Cañas* geniculadas a erectas, ramificadas en los nudos inferiores; entrenudos de 1.5–10 cm de largo, cilíndricos, los inferiores comprimidos, glabros a híspidos en la porción superior, con tintes violáceos; nudos glabros a cortamente pilosos. *Vainas* de 2–7 cm de largo, glabras a hirsutas, con pelos caedizos, un borde papiloso-pestañoso en toda su extensión o sólo hacia la porción distal, el restante glabro. *Lígulas* membranáceo-pestañosas, de 0.7–1.8 mm de largo; cuello glabro. *Láminas* lanceoladas a linear-lanceoladas, de 2–18 cm de largo, 0.3–1.7 cm de ancho, más o menos erectas, ascendentes, planas, glabras o con la cara abaxial esparcidamente pilosa, de base redondeada y ápice agudo, con los bordes finamente escabriúsculos, los basales pestañosos. *Pedúnculos* hasta de 30 cm de largo, glabros a esparcidamente pilosos. *Inflorescencias* terminales, laxas, difusas, de 3.5–23 cm de largo, 1.5–11 cm de ancho; *eje principal* y ejes de las ramificaciones glabros, escabriúsculos; ramificaciones de primer orden alternas a subopuestas, divergentes; ramificaciones de segundo orden adpresas con espiguillas apretadas sobre los ejes, próximas; pulvínulos glabros; pedicelos claviformes, de 1–4 mm de largo, escabriúsculos, cortamente pilosos hacia el ápice a glabros. *Inflorescencias axilares* presentes, similares a las terminales. *Espiguillas* elipsoides, de 2.4–3(–4.5) mm de largo, 0.7–0.9(–1.5) mm de ancho, de ápice largamente acuminado, sin estípite basal, verdosas a cobrizas o con tintes purpúreos; gluma superior y lemma inferior subiguales, 0.7–0.9(–1.8) mm más largas que el antecio superior. *Gluma inferior* ovado-acuminada, de 1.2–1.8(–2.7) mm de largo, ½–¾ del largo de la espiguilla, 5–7-nervia, el nervio medio escabriúsculo. *Gluma superior* de 2.2–2.7(–3.3) mm de largo, 7–9(–11)-nervia; gluma inferior y gluma superior separadas por un corto entrenudo de 0.3 mm de largo. *Lemma inferior* glumiforme, de 2.1–2.8(–3.9) mm de largo, 7–9(–11)-nervia. *Pálea inferior* ausente o reducida, cuando presente anchamente lanceolada, de 0.2–0.9 mm de largo, 0.2–0.3 mm de ancho, 1/7–½ del largo del antecio superior, de ápice bilobado a agudo, membranácea, hialina, glabra. *Antecio superior* obovoide a la madurez, de 1.5–1.8(–2.5) mm de largo, 0.6–0.9(–1.2) mm de ancho, crustáceo, pajizo

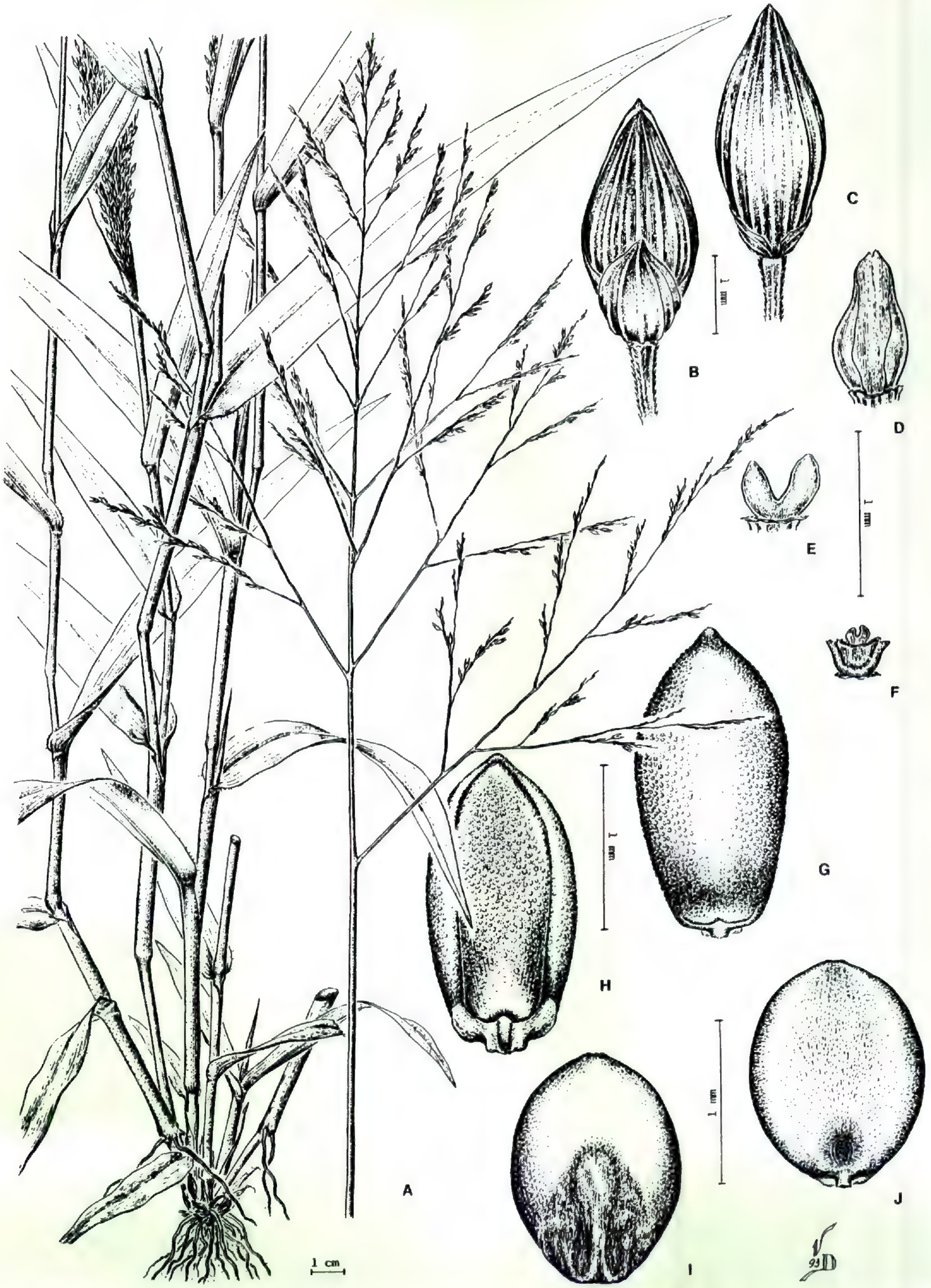


Figura 15. *Panicum alatum* var. *alatum*.—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior. D–F. Pálea inferior.—G. Antecio superior visto del lado de la lemma.—H. Antecio superior visto del lado de la pálea, con expansiones carnosas hacia la base.—I. Cariopsis, vista escutelar.—J. Cariopsis, vista hilar. (A–H, *Gentry 14353*; I, J, *Hinton et al. 6423*.)

a castaño oscuro a la madurez, liso, fuertemente papiloso en toda su superficie o con papilas presentes sólo hacia el ápice de la pálea, cortamente estipitado, con dos expansiones carnosas basales de 0.3–0.4 mm de largo, castaño claras a la madurez; lemma 7-nervia. *Cariopsis* ovoide, de 1–1.2(–1.7) mm de largo, 0.6(–1) mm de ancho, blanquecino; hilo punctiforme; embrión ½ del largo de la cariopsis.

Esta nueva especie se distingue de *Panicum hirticaule* por tener antecio superior obovoide, cortamente estipitado y con dos expansiones carnosas en su base.

1a. **Panicum alatum** var. **alatum**

Espiguillas de 2.5–3 mm de largo. *Gluma inferior* 1.4–1.8 mm de largo. *Gluma superior* y *lemma inferior* 0.7–0.9 mm más largas que el antecio superior. *Antecio superior* opaco, fuertemente papiloso en toda su superficie.

Distribución y ecología. Sur de los Estados Unidos de América y norte de México (Fig. 3), en lugares abiertos, rocosos, ocasional en bordes de arroyos en lugares húmedos, desde el nivel del mar hasta los 1220 m.

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **Arizona**: Phoenix, 25 Sep. 1904, *Griffiths 7317* (US). **California**: overflow land along Colorado River, 1 dic. 1905, *Schellenger 3* (LA). Sin estado: E of Desert Center, 16 Sep. 1929, *Jones 24493* (MO); Gila bottom, *Schott 16* (MO). MEXICO. **Baja California Sur**: Purísima, 17 Feb. 1889, *Brandegee 8* (LA, US); 12 mi. S of El Solito, 27°53′, 113°48′W, 21 Oct. 1959, *Wiggins 15135* (MEXU, MO); 11 mi. S of Millers landing, 19 Oct. 1959, *Wiggins 15097* (GH, ISC); 1 mi. SW of jct. of road to Huatamote along Hwy. Mex. # 1, 365 m, 29 ene. 1977, *Reeder & Reeder 6718* (MEXU); Cuesta de Chuenque, ca. 22 km S of Loreto on road to Puerto Escondido, 25°51′N, 111°25′W, 10 Oct. 1964, *Carter & Ferris 4726* (LA, MEXU). **Durango**: Ceballos, Zona del Silencio, 1050 m, 25 Oct. 1978, *Martínez 1313* (MEXU). **Guerrero**: Distrito Coyuca, Cutzamala, 8 Sep. 1934, *Hinton et al. 6423* (GH, NY, US); Cutzamala, 8 Sep. 1934, (GH, MO). **Michoacán**: Apatzingán, 4 mi. W of Apatzingsán, 1200 ft, 8 Aug. 1941, *Leavenworth & Hoogstraal 1371** (MO). **Nayarit**: 2 mi. SE of Las Vacas, 60-90 m, 21 Sep. 1960, *McVaugh 19291* (US). **San Luis Potosí**: 12 mi. E of Ciudad Valles, 17 July 1963, *McGregor et al. 840* (US); 2 km E of Santa Catarina along Hwy. 70, 1220 m, 23 Oct. 1978, *Reeder & Reeder 7045* (LA). **Sinaloa**: El Quelite cut-off to Rt. 15, 34 mi. S of Elota, 10 Sep. 1962, *Skorepa 116** (MO, WIS), pr. p.; Cerros Navachiste, about Bahía Topolobampo, 26/30 Sep. 1954, *Gentry 14353**,** (SI); outskirts of Topolobampo, 9 Oct. 1966, *Gould 12110** (GH, US). **Sonora**: 54.5 mi. S of Hermosillo, 21 Sep. 1974, *de Wet & Harlan 4354** (MEX, MO); 35.8 mi. SE of Guaymas along Mex. 15, 22 Sep. 1974, *de Wet & Harlan 4732* (MEXU); Guaymas, 17 Sep. 1908, *Hitchcock 3553* (US), 1887, *Palmer 208* (LA, NY, US), *346* (US); near Guaymas, on rocky, brush-covered slopes just N of Miramar Beach, 7 Oct. 1966, *Gould 12071* (LA). **Tamaulipas**: between Cerro Mante y Tampico village of Granja Trinidad, 31 Aug. 1971, *Beetle et al. M-1211* (ISC, MO). Sin localidad, 1897, *Palmer 249* (US), *251* (GH, US).

1b. **Panicum alatum** var. **longiflorum** Zuloaga & Morrone, var. nov.

TIPO: México. Baja California Sur: Mesa del Potrero de San Javier (NE of Misión San Javier), ca. 25°52′N, 111°32.5′W, 19 Sep. 1965, *Carter 4970**,** (holótipo, MO; isótipos, GH, LA, MEXU).

Panico alato var. *alato* affine sed spiculis 3.6–4.5 mm longis, anthoecio laevi non papillato differt.

Espiguillas de 3.6–4.5 mm de largo. *Gluma inferior* de 1.9–2.7 mm de largo. *Gluma superior* y *lemma inferior* 1.2–1.8 mm más largas que el antecio superior. *Antecio superior* liso, brillante, con papilas presentes sólo hacia el ápice de la pálea.

Distribución y ecología. Ocasional en el sur de los Estados Unidos y México (Fig. 10), en ambientes abiertos, secos.

Nombre vulgar. "Zacate" (en México).

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **California**: Jamacha, 4 July 1894, *Camby 6* (US). MEXICO. **Baja California Sur**: Cerro Teombó, N of Portezuelo Gabilán, ca. 25°51′N, 111°25′W, 1 Oct. 1965, *Carter 5074*** (GH, LA, MEXU, MO); Sierra de la Giganta, *Carter 5548* (GH, LA); E side of Cañada del Encinal, S side of Valle de los Encinos, 26°03′N, 111°34′W, 1 Oct. 1967, *Carter 5374* (GH, LA, MEXU); Sierra de la Giganta, Cerro de Barreno, S side of Valle de Los Encinos, ca. 26°03′N, 111°35′W, 1260 m, 30 Sep. 1967, *Carter 5353* (LA, MEXU, SI). **Sonora**: 12 mi. W of Hermosillo, 27 Aug. 1941, *Wiggins & Rollins 127* (MO, US); sin localidad, *Hitchcock 3541 1/2* (US).

1c. **Panicum alatum** var. **minus** (Andersson) Zuloaga & Morrone, comb. nov.

Basónimo: *Panicum hirticaule* J. Presl var. *minus* Andersson, Kongl. Vetensk. Acad. Handl. 1853: 135. 1855. TIPO: Ecuador. Archipiélago de Colón: "In insula Indefatigable," mayo 1852, *Andersson s.n.* (holótipo, no visto; isótipo, GH, probables isótipos, MO-2098647, NY).

Panicum hirticaule J. Presl var. *majus* Andersson, Kongl. Vetensk. Acad. Handl. 1853: 135. 1855. TIPO: Ecuador. Archipiélago de Colón: "Hab. in insulis Chatham et Charles," mayo 1853, *Andersson s.n.* (holótipo, no visto; isótipo, GH).

Espiguillas de 2.4–3(–3.2) mm de largo. *Gluma inferior* de 1.2–2.1 mm de largo. *Gluma superior* y *lemma inferior* 0.4–0.8 mm más largas que el antecio superior. *Antecio superior* liso, brillante, con papilas hacia el ápice de la pálea.

Distribución y ecología. Ampliamente distribuida en el sur de los Estados Unidos y norte de México (Fig. 5), donde crece en suelos arcillosos o arenosos; común a lo largo de bordes de caminos. Es ocasional en El Salvador, Nicaragua y Venezuela y también se halla en las Islas Galápagos, Ecuador, donde crece en suelos rocosos. Habita desde nivel del mar hasta los 1860 m.

Material adicional examinado. ECUADOR. **Archipiélago de Colon**: Isla San Cristóbal (Chatham Island), Wreck bay, 21 Feb. 1905, *Stewart 1293* (GH, MO, NY, SI); Charles Island, May 1899, *Snodgrass & Heller 454* (GH); Española, landing site on north coast, beach area and area to El Chaco, 3 July 1986, *Lawesson 3143* (MO); Indefatigable Island, Academy Bay, 4 May 1932, *Howell 9076* (F, GH, MO, NY); Gardner Island, near Hood Island, 22 Apr. 1932, *Howell 8728* (GH, US). EL SALVADOR. **La Unión**: La Unión, 13 Nov. 1911, *Hitchcock 8794* (US). **Sonsonate**: Acajutla, 10 ago. 1951, *Rohweder 1648* (MO). ESTADOS UNIDOS DE AMERICA. **Arizona**: San Bernardino Ranch, 28 Aug. 1892, *Mearns 738* (US); Tucson, 2 Sep. 1903, *Thomber 176* (LA, MO); Santa Cruz Valley near Tucson, 20 June 1881, *Pringle 13940** (MO); Patagonia, Santa Cruz County, *Hitchcock 3675* (US); Yavapai Co., near Kirkland, 5 Oct. 1930, *Peebles et al. 7417* (LA). **California**: bed of Fort Dry Lake, 24 mi. E of Blythe, 350 ft., 30 Nov. 1937, *Grinnell & Grinnell 1082a* (JEPS, LA); E of Desert Center, 16 Sep. 1929, *Jones s.n.* (LA 406771). **New Mexico**: Gila, 29 Aug. 1880, *Greene 13107* (MO); plains of Río Gila, 29 Aug. 1880, *Greene 258* (US); Doña Ana County, Mesilla Valley, 11 Oct. 1904, *Wooton s.n.* (MO-1314437). **Texas**: El Paso, 23/24 Aug. 1915, *Hitchcock 13333* (US); sin localidad, *Nealley s.n.* (US). HONDURAS. **Valle**: 3 km N of Jícaro Galán along highway 1 to Tegucigalpa, 5 Oct. 1986, *Davidse & Pilz 31651* (MO, SI); savanna on heavy black clay, heavily grazed and disturbed, 3 airline km W of San Lorenzo along the road to Amapala, 5 Oct. 1986, *Davidse & Pilz 31704* (SI). MÉXICO. **Baja California Norte**: Sierra Juárez, 2 Oct. 1966, *Moran 13664* (MO). **Baja California Sur**: San José del Cabo, 17 Oct. 1899, *Brandegee 42* (LA, US); Llano Caquihui, Sierra de la Giganta W of Los Dolores, 24°26′N, 110°52′W, 17 Nov. 1959, *Wiggins 15510* (GH); 3.3 mi. SW of San Ignacio, 27°14′N, 112°53′W, 25 Oct. 1959, *Wiggins 15179* (LA); Sierra de la Giganta, Arroyo at NW base of Cerro Mechuda, 24°48′N, 110°44′W, 2 Nov. 1971, *Moran 18878 1/2* (LA). **Campeche**: on W edge of Escárcega in disturbed area, 21 Dec. 1972, *Reeder & Reeder 6098* (MO). **Chiapas**: Chiapa de Corzo, El Chorredero 5.6 mi. E of Chiapa de Corzo along Mexican highway 190, 2500 ft., 21 June 1966, *Laughlin 1113* (US); Mun. Tuxtla Gutíerrez, 1800 ft., 1 July 1965, *Breedlove 10630* (US); about 27 mi. NW of Mexico-Guatemala border on the road to Comitán, 900 m, 23 Aug. 1953, *Reeder & Reeder 2082* (LA, MEXU). **Chihuahua**: Chihuahua, 4800 ft., *Soderstrom 896* (US); Meoquí, 24 ago. 1935, *Le Sueur 032* (US); Llano de Chilicote 7 mi. E of Chilicote Station, 26 Sep. 1938, *Johnston 7992*, *** (GH, US). **Coahuila**: El Mesteño, Ejido 4 de Marzo, 28 July 1976, *Roig s.n.* (ANSM). **Guerrero**: 6 km al W de Colotlipa, 20 Aug. 1978, *Blanco et al. 512* (MEXU). **Jalisco**: Guadalajara, Río Grande de Santiago, 27 km E of Guadalajara, 5200 ft., 26 Aug. 1941, *Leavenworth & Leavenworth 1875* (MO); Puente Grande, 13 mi. SE of Guadalajara, on road to Aguascalientes, 5000 ft., 17 Sep. 1959, *Soderstrom 647* (US); Tecolotlán, 1500 m, 5 Oct. 1970, *Díaz Luna 2044* (MEXU). **Michoacán**: Apatzingán, jungle at La Majada, 5 mi. W of Apatzingán, 1000 m, 5 Aug. 1941, *Leavenworth & Leavenworth 1335* (US); Chavinda, 27 Sep. 1946, *Hernández Xolocotzi et al. X-2791* (US); ca. 5 mi. N of Cotija and 22 mi. S of Jiqauilpán, 6000-6200 ft., *King & Soderstrom 4679* (LA, NY, US). **Morelos**: 2 km NW of Axochiapan, 10 Aug. 1950, *Walther 63* (US); 12 km NW of Axochiapan, 3500 ft., 10 Aug. 1950, *Lyons Jr. 59* (US) *83* (MEXU, US). **Oaxaca**: Tomellin, 14 Aug. 1910, *Hitchcock s.n., Amer. Gr. Hb. 28* (LA, US); 12 km NE of the city of Tehuantepec, along the Pan-American highway (routes 185 & 190), 50 m, 7 July 1958, *King 391* (US). **San Luis Potosí**: Palma Court, Valles, 8 Aug. 1961, *Gould 9558* (ISC, LA, MO, US). **Sinaloa**: Culiacán, 27 Aug./15 Sep. 1891, *Palmer 1545* (LA, NY, SI, W), about 15 mi. SE of Villa Unión, in disturbed area along the road, 23 Sep. 1953, 90 m, *Reeder & Reeder 2430* (LA, US); vicinity of Labradas, 18 Sep. 1925, *Ferris & Mexía 5070* (MEXU); sin localidad, 27 Aug. 1891, *Palmer 1554* (F, NY). **Sonora**: 10 mi. S of Hermosillo, 17 Sep. 1908, *Hitchcock 3541* (US); Guaymas, 17 Sep. 1908, *Hitchcock 3547* (US); Pinacate Junction, Pinacate Region, 7.5 km E of Los Vidrios, 31°59′N, 113°21′W, 215 m, 14 Sep. 1986, *Felger 86-339* (MEXU). **Tamaulipas**: en los alrededores de Ciudad Mante, *Sánchez-Ken & Nieto M. 430* (MEXU). **Veracruz**: Puente Nacional Veracruz, carretera Jalapa–Veracruz, Emiliano Zapata, 250 m, 10 ago. 1982, *Dorantes et al. 1510* (F, MEXU). **Sin estado**: sin localidad, *Palmer s.n.* (US). NICARAGUA. **León**: Puente Izapa, km 60 carretera a León, 12°15′W, 86°44′W, 13 jul. 1981, *Moreno 9838* (MO). VENEZUELA. **Zulia**: Guarero, Guajira, 25 dic. 1954, *Vareschi 3745* (VEN).

El ejemplar *Wiggins 15179* comprende plantas sumamente pequeñas, de 1.5 a 6 cm de alto.

Los ejemplares *Hitchcock 8794, Davidse & Pilz 31651, 31704,* incluidos en esta variedad, se distinguen por poseer un rizoma en su base, constituyendo los únicos especímenes aparentemente perennes de esta especie.

Reeder & Reeder (1971) ubican a *P. hirticaule* var. *majus* y var. *minus* Andersson en la sinonimia de *P. hirticaule.*

2. Panicum aquarum Zuloaga & Morrone, Novon 1: 185, figs. 1, 2. 1991. TIPO: Venezuela. Guárico: Dpto. Infante, Parque Nacional Aguaro-Guariquito, Congriales de la Gorra, entre La Esperanza y Mesa de Cambao, ca. 9°12′–9°16′N y 67°48′–67°60′W, 60 m, dic. 1981, *Delascio, Montes & Davidse 11206* (holótipo, VEN; isótipos, MO, SI). Figura 16.

Plantas anuales?, de 0.90–1.30 m de alto. *Cañas* erectas, arraigadas en los nudos inferiores y manifiestamente ramificadas en los nudos superiores; entrenudos de 7–19 cm de largo, glabros, estriados, huecos; nudos glabros, comprimidos, castaños. *Vainas* de 8–18 cm de largo, delgadas, glabras, lustrosas en la cara adaxial y con aerénquima, los márgenes membranáceos. *Lígulas* ca. 1.2 mm de

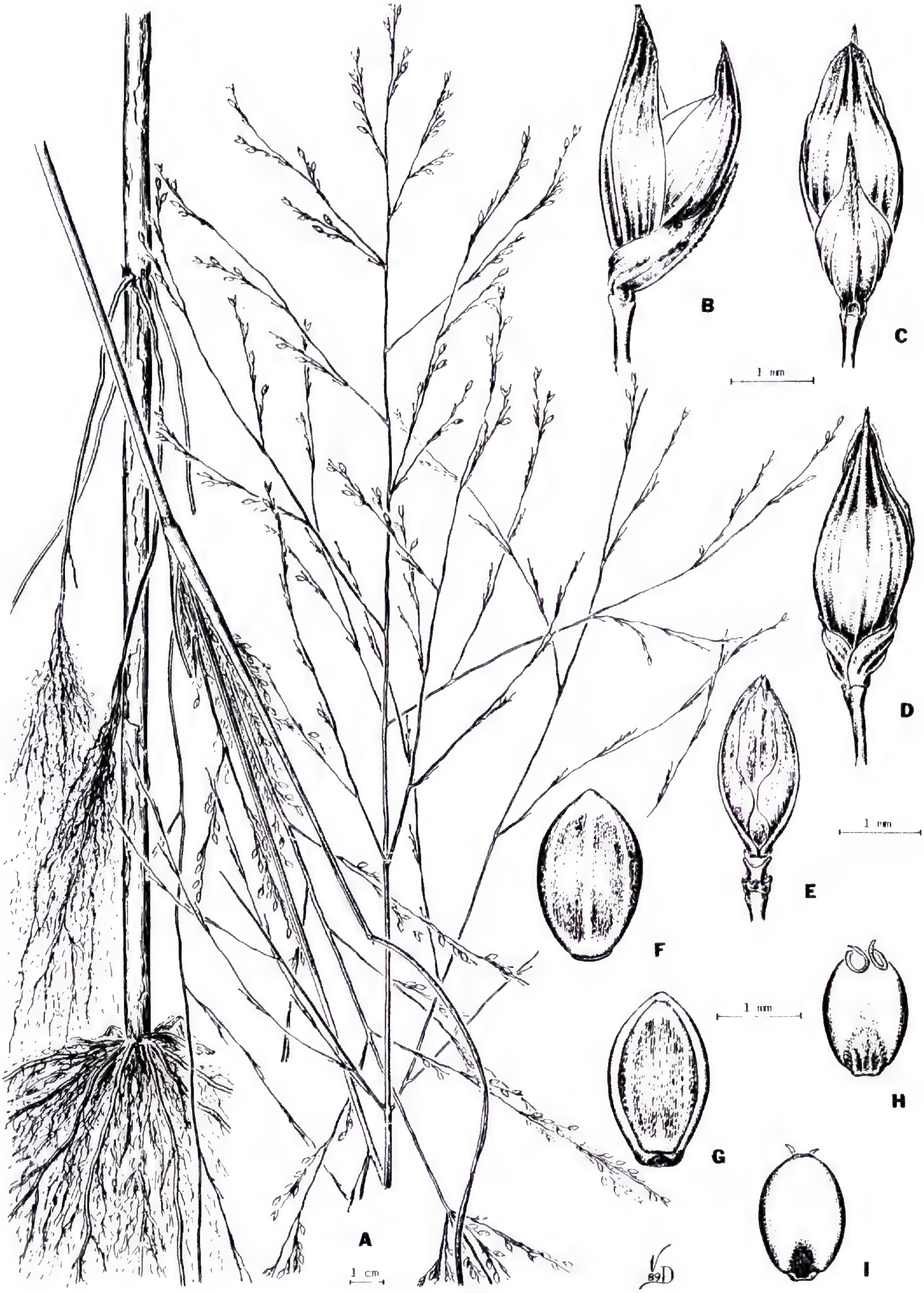


Figura 16. *Panicum aquarum*.—A. Hábito.—B. Espiguilla, vista lateral.—C. Espiguilla vista del lado de la gluma inferior.—D. Espiguilla vista del lado de la gluma superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Cariopsis, vista escutelar.—I. Cariopsis, vista hilar. (*Blydenstein 1846.*)

largo, cortamente membranáceas en la base y largamente ciliadas en el ápice, la cara adaxial pilosa; cuello glabro. *Láminas* lineares, de 11–18 cm de largo por 0.2–0.4 cm de ancho, las inferiores deciduas, glabras, angostadas hacia la base, los márgenes escabriúsculos, con nervio medio manifesto en la zona basal. *Pedúnculos* hasta de 25 cm de largo, escabriúsculos. *Inflorescencias* terminales, piramidales, laxas, multifloras, de 35–40 cm de largo por 12–20 cm de ancho; *eje principal* cilíndrico, glabro; pulvínulos glabros; ramificaciones de primer orden alternas o subopuestas, divergentes; ejes de las ramificaciones triquetros, escabriúsculos; ramificaciones de segundo y tercer orden alternas con ejes escabriúsculos; espiguillas congestas sobre las ramificaciones de tercer orden; pedicelos claviformes, glabros. *Inflorescencias axilares* numerosas, menores, similares a la inflorescencia terminal. *Espiguillas* solitarias, elipsoides, de 3–3.9 mm de largo, 1–1.2 mm de ancho, estipitadas, glabras, pajizas y con tintes violáceos, abiertas a la madurez; gluma superior y lemma inferior subiguales, acuminadas, superando en largo al antecio superior. *Gluma inferior* ovada, abruptamente acuminada, de 1.7–2.7 mm de largo, ½ a ¾ del largo de la espiguilla, (3–)5-nervia, el nervio medio escabriúsculo hacia la porción superior; entrenudo conspicuo entre la gluma inferior y la gluma superior. *Gluma superior* de 3–3.6 mm de largo, acuminada, (5–)7-nervia. *Lemma inferior* glumiforme, de 3–3.2 mm de largo, (5–)7-nervia. *Pálea inferior* oblongo-lanceolada, de 1.7–2.1 mm de largo, 0.6–1 mm de ancho, tan larga a ligeramente menor que el antecio superior, glabra, hialina. *Antecio superior* elipsoide, de 2.1 mm de largo, 1.2–1.3 mm de ancho, crustáceo, pajizo, con manchas negruzcas a la madurez, con un anillo castaño en la base; lemma superior 5-nervia, los márgenes involutos; pálea superior 2-nervia, con papilas verrugosas hacia el ápice. *Cariopsis* anchamente elipsoide, 1.5 mm de largo, 1 mm de ancho, blanquecina; hilo subbasal, punctiforme; embrión ⅓ o menos del largo de la cariopsis.

Distribución y ecología. Restringida al extremo norte de América del Sur, Brasil, Colombia y Venezuela (Fig. 6). Habita en lugares inundados; florece y fructifica entre septiembre y mayo.

Material adicional examinado. BRAZIL. **Amazonas**: Mun. Humaitá, 7°31′S, 63°10′W, campo a 15–17 km da cidade pela estrada 319 ao norte da estrada, entre igarapés Retiro e Bom Futuro, 70 m, 11 mayo 1980, *Gemtchujnicov & Janssen 369* (IBGE, SP). **Pará**: Marajó, Camará River, Sep. 1902, *without collector* (US-1024781); ad Tocantins flumen inter Porto Imperial et Funil, *Burchell 8813* (K, W). COLOMBIA. **Meta**: Lago Carimagua, altillanura plana, bajo 30 cm de agua, 19 nov. 1963, *Blydenstein 1846* (COL, G).

Panicum aquarum se ubica dentro de la sección *Panicum* por compartir caracteres similares de espiguillas y aspectos anátomicos. Difiere del resto de las especies de esta sección por ser una planta acuática, con aerénquima en las vainas y láminas decíduas hacia la base. Se caracteriza asimismo por poseer espiguillas abiertas a la madurez, con gluma superior y lemma inferior (5–)7-nervias.

3. Panicum aztecanum Zuloaga & Morrone, sp. nov. TIPO: México. México: Temascaltepec, Bejucos, barranca, 610 m, 7 Oct. 1932, *Hinton 2010** (holótipo, US; isótipos, MEXU, MO, NY). Figura 17.

Panico lepidulo affine sed foliis linearibus usque ad filiformes, spiculis stipitatis, conspicuo internodo inter inferiorem et superiorem glumam differt.

Plantas perennes, cespitosas. *Cañas* erectas de 50–100 cm de alto, paucinodes, ramificadas en la base; entrenudos de 13–16 cm de largo, 1 mm diám., glabros, violáceos hacia la porción superior; nudos glabros, oscuros. *Vainas* de 2–10 cm de largo, más cortas que los entrenudos, glabras a esparcidamente pilosas, con pelos delicados, sedosos, los márgenes membranáceos, glabros, largamente pestañosos junto a la unión de la lámina, con pelos blanquecinos, sedosos, hasta de 3.6 mm de largo. *Lígulas* membranáceo-ciliadas, de 0.4–0.6 mm de largo; cuello glabro a largamente piloso. *Láminas* lineares a filiformes, de 14–30 cm de largo, 0.1–0.3 cm de ancho, involutas, excepcionalmente planas, con ambas caras o con la cara adaxial esparcidamente pilosa, de base angostada continuándose imperceptiblemente con la vaina, el ápice largamente agudo, los márgenes escabriúsculos, pestañosos hacia la base. *Pedúnculos* largamente exertos, hasta de 48 cm de largo, glabros, con tintes violáceos. *Inflorescencias* terminales, exertas, laxas, difusas, de 15–18 cm de largo, 8–10 cm de ancho; *eje principal* glabro, escabriúsculo hacia la porción basal, liso en el resto de la superficie; ramificaciones de primer orden ascendentes, flexuosas, divergentes, desnudas hacia la base; ramas de segundo orden con 2–3 espiguillas solitarias hacia el ápice; pulvínulos glabros; pedicelos de 2–20 mm de largo. *Espiguillas* largamente elipsoides, de 3.7–4.5 mm de largo, 1.5 mm de ancho, agudas, glabras, purpúreas, estipitadas; gluma superior y lemma inferior subiguales, 1.2–1.5 mm más largas que el antecio superior. *Gluma inferior* ovado-acuminada, de 2–3 mm de largo, ½–¾ del largo de la espiguilla, 7-nervia, el nervio medio escabriúsculo.

Figura 17. *Panicum aztecanum.*—A. Hábito.—B. Detalle de la región ligular.—C. Espiguilla vista del lado de la gluma inferior.—D. Espiguilla vista del lado de la gluma superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Cariopsis, vista escutelar.—I. Cariopsis, vista hilar. (A, B, *Hinton 2010*; C–I, *Rzedowski 17449*.)

Gluma superior de 3.2–4.2 mm de largo, la cara interna escabriúscula hacia el ápice, 7–9-nervia; gluma inferior y gluma superior separadas por un entrenudo de 0.5 mm de largo. *Lemma inferior* glumiforme, de 3–4 mm de largo, 7–9-nervia. *Pálea inferior* lanceolada, de 1.7–2.7 mm de largo, 0.6 mm de ancho, ¾ del largo del antecio superior, membranácea, hialina, glabra. *Antecio superior* ovoide, de 2.4–3 mm de largo, 0.9–1.2 mm de ancho, crustáceo, liso, lustroso, pajizo, sin cicatrices en la base, de base circular, pálida a la madurez; lemma 7-nervia; pálea con papilas simples y micropelos globosos hacia el ápice. *Cariopsis* ovoide, de 1.8 mm de largo, 1 mm de ancho, blanquecina; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Endémica de México (Fig. 7), se encuentra en bosques de *Pinus* y *Quercus*, en laderas, entre los 600 y 1600 m. Florece y fructifica entre agosto y octubre.

Material adicional examinado. MEXICO. **Distrito Federal**: cerca de la pirámide de Cuicuilco, *Rzedowski 2047** (US). **Jalisco**: 4.5 mi. N–NE of Talpa de Allende, 1450–1500 m, 17 Oct. 1960, *Mc Vaugh 20345**,** (US, 2 hojas); Mun. Tecalitlán, Llano Verde, cerca de los Corrales, Sierra de los Corrales, 1600 m, 24 oct. 1963, *Rzedowski 17423, 17449* (US); Mun. Tecalitlán, Barranca de San Juan de Dios, cerca de los Corrales, Sierra de los Corrales, 1300 m, 23 oct. 1963, *Rzedowski 17367* (US). **Sinaloa**: Santa Lucía, E of Panuco, 900–1200 m, 28 ago. 1935, *Pennell 20033* (US).

Especie afín a *Panicum lepidulum* de la que se distingue por tener láminas lineares a filiformes, largamente pestañosas junto a la unión de la vaina y espiguillas estipitadas y con un entrenudo manifiesto entre la gluma inferior y superior.

4. Panicum bergii Arechavaleta, Anales Mus. Nac. Montevideo 1: 147. 1894. Las Gramíneas Uruguayas: 127. 1894. TIPO: Uruguay. "Campos del Departamento de Montevideo, San José, Florida, Mercedes, etc." (holótipo no hallado; probable isótipo, US-974426). Figura 18.

Plantas perennes, cespitosas, de (10–)30–70(–140) cm de alto, con catáfilos pilosos. *Cañas* geniculados, erectas, ramificadas en los nudos inferiores y medios; entrenudos de 2–15 cm de largo, cilíndricos, huecos, pilosos, con pelos tuberculados, más abundantes hacia la porción inferior; nudos violáceos, pilosos a glabros. *Vainas* estriadas, pajizas, glabrescentes a densamente híspidas, los bordes membranosos, pestañosos. *Lígulas* membranáceas en la base, luego largamente ciliadas, de 1–3 mm de largo; cuello pajizo, con pelos tuberculados a glabro. *Láminas* linear-lanceoladas, de (3–)8–35(–60) cm de largo, 0.2–1.2 cm de ancho, densamente híspidas, con largos pelos blanquecinos, a glabrescentes, de base atenuada y ápice agudo, bordes escabrosos e involutos a planos, el nervio medio manifiesto. *Pedúnculos* subincluidos a largamente exertos, glabros a híspidos. *Inflorescencias* laxas, difusas, piramidales, de (4–)15–30(–40) cm de largo, (3–)10–25 cm de ancho, caedizas a la madurez como una unidad; ramas divergentes del raquis, las inferiores en verticilo, las superiores opuestas o alternas; *eje principal* densamente híspido, con pelos blanquecinos largos, a glabros, escabroso, triquetro; ejes de las ramificaciones triquetros, glabros a híspidos, pulvínulos pilosos a glabros; pedicelos triquetros, escabrosos, de 3–20 mm de largo. *Espiguillas* ovoides, de 2.1–2.9 mm de largo, 0.8–1.2 mm de ancho, sin estípite basal, glabras, pajizas, con tintes violáceos, gluma superior y lemma inferior subiguales, 0.3 mm más largas que el antecio superior. *Gluma inferior* ovada, de 1–1.6 mm de largo, acuminada, 5-nervia, el nervio medio escabriúsculo hacia el ápice. *Gluma superior* de 2.1–2.8 mm de largo, 7–9-nervia, nervio medio escabriúsculo hacia el ápice. *Lemma inferior* de 2–2.7 mm de largo, 7–9-nervia. *Pálea inferior* elíptica, de 1.4–2.2 mm de largo, 0.6–1 mm de ancho, tan larga como el antecio superior, hialina, glabra, con los bordes finamente ciliados. *Antecio superior* ovoide, de 1.5–1.9 mm de largo, 0.7–1 mm de ancho, crustáceo, liso, glabro, lustroso, pajizo, castaño a la madurez, con dos cicatrices basales de 0.1 mm de largo, castañas a la madurez; lemma superior 7-nervia, con aguijones en el ápice; pálea con papilas simples hacia el ápice. *Cariopsis* elipsoide, de 1.2–1.4 mm de largo, 0.7–1 mm de ancho; hilo punctiforme, embrión la mitad del largo de la cariopsis.

4a. Panicum bergii var. **bergii**

Panicum pilcomayense Hackel, Bull. Herb. Boissier, sér. 2, 7: 449. 1907. TIPO: Paraguay: "Ad margines silvarum in regione cursus inferioris fluminis Pilcomayo, flor. mens: Maj. 1906, *Rojas n. 105*** (holótipo, W; fragmento, BAA, US-80948; isótipos, G. P, US-974440).

Panicum bergii Arechavaleta f. *convoluta* Palacios en Burkart, FL. II. Entre Ríos, Colec. Cient. INTA 6(2): 309. 1969. TIPO: Argentina. Entré Ríos: Concepción del Uruguay, *Burkart 22915* (holótipo, SI).

Panicum burkartii Zuloaga, Bol. Soc. Argent. Bot. 17: 179, fig. 1. 1976. TIPO: Argentina. Buenos Aires: Cerro Copelina, Mar del Plata, 1932, *Hicken s.n.* (holótipo, SI-13460).

Vainas y *láminas* esparcidamente pilosas a glabrescentes. *Inflorescencias* con el eje principal y ramificaciones glabros.

Distribución y ecología. Especie sudamericana,

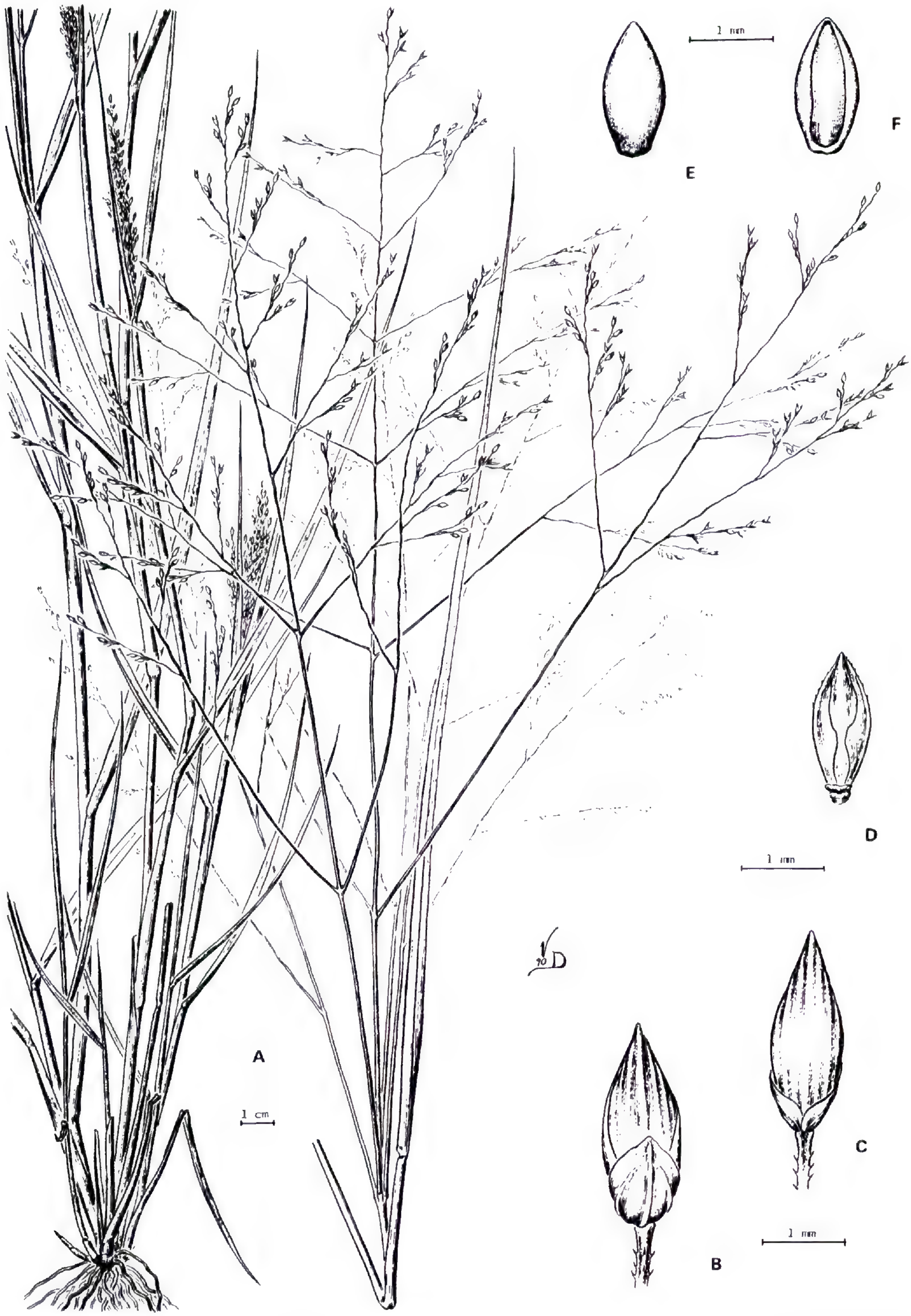


Figura 18. *Panicum bergii.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Pálea inferior.—E. Antecio superior visto del lado de la lemma.—F. Antecio superior visto del lado de la pálea. (A, *Cabrera & Zuloaga 32328*; B–F, *Rojas 2358.*)

ampliamente distribuida en Argentina, Paraguay, Uruguay y el sur del Brasil (Fig. 6). Menos frecuente en el NE del Brasil, Guayana y Venezuela; introducida en los Estados Unidos de América. Habita en campos, en lugares abiertos y relativamente secos.

Nombre vulgar. "Paja voladora" (Palacios en Burkart, 1969; Cabrera, 1970; Rosengurtt et al., 1970).

Material representativo citado. ARGENTINA. **Buenos Aires**: Maipu, *Krapovickas 2906* (F, LIL, MO, SI). **Chaco**: Ruta 16, 4 km from Belgrano bridge, *Renvoize et al. 3583* (MO, SI). **Córdoba**: Manfredi, *Krapovickas 6681* (GH, SI). **Corrientes**: Río Miriñay y Ruta 23, *Quarín 1639* (CTES, SI, US). **Entre Ríos**: 2–3 km al N de Ceibas, *Troncoso et al. 2638* (SI, US). **Formosa**: Ruta 11 vieja, al N de Arroyo Francesa Cué, *Guaglianone et al. 360* (MO, SI, US). **Jujuy**: Sierra de Zapla, Mina 9 de Octubre, *Cabrera et al. 32704* (SI). **La Pampa**: Anguil, *Steibel 2451* (SI, US). **Misiones**: Ruta Prov. 105, Villalonga, *Zuloaga et al. 2323** (MO, SI). **Santa Fe**: Las Toscas, Quarín 110 (CTES, SI). **Santiago del Estero**; Ruta 34, 11 km al SE de Argentina, *Rotman et al. 100*** (SI, US). **Tucumán**: Las Cejas, *Venturi 2539* (LIL, SI, US). BOLIVIA. **La Paz:** Prov. Iturralde, Luisita, sabana húmeda, W del Río Beni, *Beck & Haase 9921* (K). **Santa Cruz**: University Farm, "El Vallecito," *Tollersey 2626* (K). BRASIL. **Pernambuco**: Tapera, *Pickel 1403* (F, US). **Rio de Janeiro**: São Pedro, 10 dic. 1929, *Chase 10151* (F, MO, RB, US). **Rio Grande do Sul**: Boca do Monte, *Palacios y Cuezzo 4368* (MO). **Roraima**: bei der Serra do Mel, *Ule 8014* (G, IAN, K, NY, US). ESTADOS UNIDOS DE AMERICA. **Alabama**: Mobile, Aug. 1891, *Mohr s.n.* (US). **Georgia**: weed around grass plots, Experiment Station, Tifton, 4 Aug. 1938, *Swallen* 5393 (US). **Texas**: Galveston Co., just N of Dollar Point, ca. 3 mi. N of Texas City, 24 Apr. 1974, *Waller & McAden 2643* (MO). GUAYANA. Sin localidad, *Schomburgk 656* (G, K, US), 701 (US). PARAGUAY. **Alto Paraguay**: Puerto Casado, dic. 1916, *Rojas 2358* (SI). **Central**: Asunción, S de Villa Hayes, *Rojas 2762* (US). **Chaco**: en palmar al SW de Villa Hayes, *Rosengurtt B-5623* (K). **Concepción**: Villa Concepción, 23 mayo 1876, *Balansa 12* (G). **Misiones**: San Juan a San Ignacio, km 208, *Burkart 18643* (SI). **Paraguarí**: Cerro Peró, feb. 1875, *Balansa 15* (G, P). **Presidente Hayes**: El Pedernal, al S de Concepción, *Burkart 18397* (SI). PERU. **Loreto**: Salinas de Pilluana, Huallaga, *Ule 6857* (G, K). URUGUAY. **Canelones**: Toledo, *Legrand 1455* (F). **Cerro Largo**: Río Negro, *Gallinal et al. PE-1290* (US). **Flores**: Río Yí y Arroyo Marincha, *Rosengurtt B-480* (US). **Paysandú**: Paysandú, *Rosengurtt B-2228* (RB, US). **Montevideo**: Montevideo, *Archavaleta 24a* (US). **Rocha**: Palmar near Chafalote, 7 km NW of 19 de Abril, *Bartlett 21345* (GH). **San José**: Kiyu, *Del Puerto 685* (F). **Soriano**: Arroyo Grande, *Herter 544* (F, GH, M, MO, NY, US). **Tacuarembó**: Camino a Rivera, 32 km de Tacuarembó, *Cabrera & Zuloaga 32416* (MO, SI). VENEZUELA. **Apure**: Llanos del Alto Apure, *Jahn 197* (US). **Monagas**: Alrededores de Jusepín, *Garófalo 381* (VEN). **Miranda**: 4 km W of Santa Teresa, *Killip & Tamayo 37046* (F, US). **Portuguesa**: carretera Barinas–Guanare, km 301, *Stergios 6935* (MO, PORT, SI).

Esta especie tiene una marcada variabilidad en lo que respecta al tamaño de las plantas, órganos vegetativos e inflorescencias. Anteriormente se caracterizaron los ejemplares de mayor porte como *P. pilcomayense*; los mismos crecen profusamente en el N de la Argentina y el Paraguay y existen ejemplares aislados en Venezuela, Guayana y el N del Brasil. Ejemplares menores fueron descritos, para el límite austral de distribución de la especie, como *P. burkartii.* Luego de examinar abundante material de este taxon se mantiene el criterio (anteriormente enunciado por Zuloaga, 1989) de considerar a *P. bergii* como la especie válida.

Panicum bergii se caracteriza, junto con *P. capillare* L., por poseer una inflorescencia quebradiza en la base a la madurez, lo que facilita la dispersión de toda la panoja como una diáspora. Este carácter fue citado por Palacios (1969), Nicora (1978) y Zuloaga (1989).

Panicum bergii fue introducida durante este siglo en los Estados Unidos de América, donde crece en el estado de Texas (Correll & Johnston, 1970, bajo *P. pilcomayense*).

4b. Panicum bergii var. **pilosissimum** Zuloaga, Hickenia 1(27): 151. 1978. TIPO: Argentina. Misiones: San José, Escuela Agrotécnica Pascual Gentilini, *Cabrera et al. 28691* (holótipo, SI).

Vainas y *láminas* densamente híspidas. *Inflorescencias* con el eje principal y ramificaciones densamente híspidas.

Distribución y ecología. Brasil, en Rio Grande do Sul y la Argentina, hallándose en las provincias de Misiones y Corrientes (Fig. 8). Crece en campos.

Material adicional examinado. ARGENTINA. **Corrientes**: Arroyo Chimiray, *Krapovickas et al. 25201** (CTES, SI); de Azara a Santo Tomé, *Zuloaga & Deginani 547* (LP). **Misiones**: Apóstoles, *Burkart 14367* (SI); Escuela Agrotécnica Pascual Gentilini, Cerro Ceferino, *Zuloaga et al. 3271** (SI); Loreto, *Montes 3478* (SI); Posadas, Establecimiento Santa Inés, *Parodi 4490* (BAA), *Canonero 92* (BAA). BRASIL. **Rio Grande do Sul**: Tupaceretan, *Rambo 9845* (US).

5. Panicum capillare L., Sp. Pl. 1: 58. 1753. *Millium capillare* (L.) Moench, Methodus: 203. 1794. *Chasea capillaris* (L.) Nieuwl., Amer. Midl. Naturalist 2: 64. 1911. *Leptoloma capillaris* (L.) Smyth, Trans. Kansas Acad. Sci. 25: 86. 1913. TIPO: Estados Unidos de América. Virginia: sin localidad, *Clayton 454* (lectótipo designado por Hitchcock (1908) BM no visto, fragmento US-80553).

Panicum bobarti Lam., Encycl. 4: 748. 1798. TIPO: Estados Unidos de América. Virginia: sin lo-

calidad, *Bobarti s.n.* (holótipo, P, fragmento y foto, US-80487).

Panicum capillare L. var. *agreste* Gattinger, Tennessee Fl.: 94. 1887. TIPO: Estados Unidos de América. Tennessee: Ridgetop, Summer Co., 14 Sep. 1882, *Gattinger s.n.* (lectótipo designado por Hitchcock & Chase (1910), TENN no visto, fragmento y foto US-80554).

Panicum capillare L. var. *vulgaris*[e] Scribner, Tenn. Agr. Exp. Sta. Bull. 7: 44. 1894, nom. illeg. superfl. TIPO: Estados Unidos de América. Tennessee: Knoxville, sin colector, no visto.

Panicum capillare L. var. *brevifolium* Vasey in Rydb. & Shear, U.S.D.A. Div. Agrostrol. Bull. 5: 21. 1897, non *P. brevifolium* L., 1753. TIPO: Estados Unidos de América. Montana: Gallatin, Manhattan, on a shaded sand bar in the Gallatin River, 19 July 1895, *Shear 436* (holótipo, US-80525).

Panicum barbipulvinatum Nash, Mem. New York Bot. Gard. 1: 21. 1900. *Leptoloma barbipulvinata* (Nash) Smyth, Trans. Kansas Acad. Sci. 25: 86. 1913. *Milium barbipulvinatum* (Nash) Lunell, Amer. Midl. Naturalist 4: 212. 1915. *Panicum capillare* L. subsp. *barbipulvinatum* (Nash) Tzvelev, Novosti Sist. Vyssh. Nizh. Rast. 1968: 18. 1968. *Panicum capillare* L. var. *barbipulvinatum* (Nash) McGregor, Phytologia 55: 256. 1984. TIPO: Estados Unidos de América. Wyoming: Yellowstone Park, Lower Geyser Basin, 4 Aug. 1897, *Rydberg & Bessey 3544* (holótipo, NY no visto).

Panicum elegantulum Suksdorf, Werdenda 1: 16. 1927, non *P. elegantulum* Mez 1917. SÍNTIPOS: Estados Unidos de América. Washington: Spokane, 14 Sep. 1916, *Suksdorf 9069*; Washington, 6 Sep. 1924, *Suksdorf 11792* (isosintipo de *Suksdorf 9069*, US-1061914 no visto).

Panicum barbipulvinatum var. *hirsutipes* Suksdorf, Werdenda 1: 17. 1927. TIPO: Estados Unidos de América. Washington: north bank of the Spokane River, near Spokane Bridge, 14 Sep. 1916, *Suksdorf 9068* (holótipo, WS no visto; isótipo, US-1061913 no visto).

Panicum capillare L. var. *occidentale* Rydb., Contr. U.S. Natl. Herb. 3: 186. 1895. TIPO: Estados Unidos de América. Nebraska: Grant Co., Whitman, 19 Sep. 1893, *Rydberg 1788* (isótipo, US-20894).

Plantas anuales, cespitosas, herbáceas, de 30–80 cm de alto. *Cañas* erectas a subgeniculadas en la base, ramificadas en los nudos inferiores y medios, cilíndricas, pajizas y con tintes violáceos, pilosas con pelos de base tuberculada más abundantes hacia la porción superior del entrenudo; entrenudos de 2.4–7 cm de largo; nudos violáceos, cubiertos de pelos blanquecinos. *Vainas* pajizas, mayores que los entrenudos, de 2–10 cm de largo, estriadas y cubiertas de largos pelos de base tuberculada. *Lígulas* membranáceo-ciliadas, de 0.9–1.5 mm de largo, con un borde pestañoso, el restante glabro; cuello castaño, piloso. *Láminas* linear-lanceoladas, planas, de 5–26 cm de largo, 0.4–1.5 cm de ancho, delgadas, de base subcordada, híspidas, con bordes escabrosos, los basales con pelos tuberculados caducos. *Pedúnculos* largamente exertos a la madurez, hasta de 30 cm de largo, aplanados, frágiles, pajizos o con tintes violáceos, glabros a esparcidamente pilosos junto al ápice. *Inflorescencias* laxas, difusas, piramidales, de 13–37 cm de largo, 7–24 cm de ancho, incluidas cuando jóvenes en las vainas superiores, luego exertas, desprendiéndose la panoja de la caña a la madurez por ruptura del eje; las espiguillas dispersas sobre las ramas; *eje principal* escabroso, triquetro, densamente híspido en la porción inferior y esparcidamente híspido hacia el ápice de la panoja; pulvínulos pilosos; ramificaciones de primer orden alternas, menos frecuentemente opuestas o verticiladas, divaricadas; ramificaciones de segundo orden divergentes; eje de las ramificaciones escabroso; pedicelos pilosos, escabrosos, de 0.5–2.8 cm de largo. *Espiguillas* angostamente elipsoides a lanceoladas, de 2.0–2.8(–3.2) mm de largo, 0.5–1 mm de ancho, de ápice largamente agudo, no estipitadas, glabras, pajizas, con tintes violáceos; gluma superior y lemma inferior subiguales, superando 0.8–1.2 mm en largo al antecio superior. *Gluma inferior* de (0.9–)1.2–1.6 mm de largo, ½ del largo de la espiguilla o algo menor, 3–5-nervia, de ápice agudo. *Gluma superior* de 1.8–2.7(–3.1) mm de largo, 7–9-nervia, nervio medio escabriúsculo. *Lemma inferior* de 1.9–2.6(–3) mm de largo, glumiforme. *Pálea inferior* ausente o vestigial, cuando presente bilobada, hasta de 0.3 mm de largo, aproximadamente ⅕ del largo del antecio superior. *Antecio superior* elipsoide, de 1.5–1.9 mm de largo, 0.5–0.8 mm de ancho, crustáceo, glabro, lustroso, pajizo, castaño a la madurez, sin cicatrices basales; lemma superior 7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* anchamente elipsoide, de 1.3–1.5 mm de largo, 0.7–1 mm de ancho; hilo punctiforme; embrión la mitad del largo de la cariopsis.

Distribución y ecología. Originaria de América del Norte. Naturalizada en Europa y América del Sur, hallándose adventicia en América del Sur en

Brasil, Uruguay, Chile y la Argentina; ocasional en Bermuda (Fig. 5). Llega hasta los 2200 m.

Material representativo citado. ARGENTINA. **Buenos Aires**: Partido Tres Arroyos, al E de la ciudad, sobre camino que conduce a la ruta 72, *Villamil 5889* (SI). **Distrito Federal**: Villa Ortuzar, *Parodi 1750* (BAA), *8218* (BAA, SI). **Entre Rios**: Isla Cambacuá, frente a Concepción del Uruguay, *Nicora 6511* (SI). **Jujuy**: Dpto. Capital, alrededores de Aeropuerto El Cadillal, *Zuloaga & Morrone 3060** (MO, SI). **La Pampa**: Estancia El Caldén, Potrero Santa Aurelia, *Rúgolo 675* (BAA, CTES). **Neuquen**: Plottier, *Ragonese s.n.* (BA 14287, BAA). **Rio Negro**: Ing. Huergo, *Burkart 15943* (BAA, SI). **San Luis**: Estación Experimental Agropecuaria San Luis-INTA, Villa Mercedes, *Anderson 2096* (BAA). BERMUDA. North Shore road, *Brown & Britton 21* (NY, US). BRASIL. **Rio Grande do Sul**: Estação estrada do Ferro, Vacaria, *Arzivenco 640* (BLA). CANADA. **Nova Scotia**: Windsor Junction, 31 Aug. 1920, *Fernald & Long 19754* (US). **Ontario**: York Co., Islington, 29 Aug. 1946, *Dore 46-137* (US). **Quebec**: Ottawa, 18 Aug. 1936, *Dore s.n.* (US-1647912). CHILE. **Bio-Bio**: Los Angeles, *Pfister 60* (LIL). **Nuble**: Recinto, *Castillo s.n.* (US-2044754). **Talca**: Talca, *Ruíz 6* (BAA). **Valparaiso**: Limache, *Garaventa 2847* (BAA). ESTADOS UNIDOS DE AMERICA. **Arizona**: near Tuba City, Coconino City, 27 Sep. 1935, *Kearney & Peebles 12868* (US). **California**: Philippsville on the Redwood hwy., 20 July 1924, *Heller 13864* (US). **Colorado**: S Platte River just W of Brighton, 4800 ft., 14 Sep. 1941, *Robbin 860* (US). **District of Columbia**: Washington, 4 Sep. 1891, *Blanchard s.n.* (US-312003). **Idaho**: Lewiston, Sep. 1929, *Gail s.n.* (US-3168275). **Illinois**: banks of Embarres river, 5 miles S of Charleston, *Macuszek 271* (LIL). **Iowa**: Palo Alto Co., Freedom Twp., sec. 8, Medium Lake, 26 Aug. 1940, *Hayden 8220* (US). **Kansas**: NW of St. Francis, *Steller & Jacobs 335* (LIL). **Kentucky**: Doyle Valley, W of Chaumont Road, 1 Oct. 1949, *Lix 738* (US). **Maine**: York Co., Occan Park, 2 Sep. 1931, *Moldenke 6377* (US). **Maryland**: near Potomac, NW of Cabin John, 5 Oct. 1904, *Chase 2726* (US). **Massachusetts**: Harwich, 29 July 1919, *Fernald & Long 17828* (US). **Missouri**: 2 miles NW of Holden, *Steyermark 72470* (LIL). **Montana**: 17 mi. above Blendive, 20 July 1883, *Ward s.n.* (US-952984). **Nebraska**: North Platte, June 1896, *Plank 38* (US). **New Jersey**: Somerset Co., Watchung, 29 Aug. 1930, *Moldenke 1372a* (US). **New Mexico**: Animas Creek, *Metcalfe 1138* (LIL). **New York**: Princes Bay, 6 Oct. 1894, *Kearney Jr. s.n.* (US-742048). **North Carolina**: sin localidad, 1885, *McCarthy s.n.* (US-952946). **North Dakota**: Morton Co., roadside between Mandan and Bismark, *Muñoz & Rollins 1006* (US). **Ohio**: Cincinnati, Spring Grove, 21 Aug. 1905, *Braun s.n.* (US-2663130). **Oregon**: MacKenzies bridge, 1740 ft., 21 July 1927, *Hitchcock 23470* (US); Roseburg, 14 July 1908, *Hitchcock 2798* (US). **Pennsylvania**: Easton, 1894, *Porter s.n.* (US-480434). **South Dakota**: Belle Fourche, 4 Aug. 1897, *Griffiths 399* (US). **Texas**: New Braunfles, 20 June 1910, *Hitchcock 5197* (US). **Vermont**: Passumpsic River, Lyndon, 11 Sep. 1931, *Fernald 519* (US). **Virginia**: Arlington, *Chase s.n.* (LIL). **Washington**: Spokane, 14 July 1908, *Chase 4986* (US). **Wyoming**: Newcastle, 24 Aug. 1897, *Griffiths 684* (US). MÉXICO. **Baja California Norte**: E of San Telmo, Rancho San José, east of San Telmo, 14 Sep. 1930, *Wiggins & Demaree 4833* (F, NY, US). **Coahuila**: Municipio de Villa Acuña, Serranías del Burro, Rancho El Bonito, ca. 29°01′N, 102°07′W, 1620 m, 18 sep. 1977, *Valdés Reyna y Riskin 1230* (ANSM). URUGUAY. **Montevideo**: Montevideo, *Felippone s.n.* (SI).

Gould (1979) indica que *P. capillare* fue citado por St. Vincent, en las Antillas, pero que no halló especímenes de esta especie en las Antillas.

Hitchcock (1951) y Davidse (1987) mencionan que en esta especie la dispersión se produce a través del conjunto de la panoja, la que es llevada por el viento a la madurez. La inflorescencia tiene en esta especie más de la mitad del largo de la planta.

6. Panicum capillarioides Vasey in Coulter, Contr. U.S. Natl. Herb. 1: 54. 1890. TIPO: Estados Unidos de América. Texas: Point Isabel, *Nealley 634* (holótipo, US-76925; probable isótipo, US-953165).

Plantas perennes, cespitosas. *Cañas* erectas de 30–75 cm de alto, simples o ramificadas en los nudos inferiores; entrenudos cilíndricos, huecos, pilosos o glabros, de 1–2 mm diám., nudos pilosos. *Vainas* iguales o menores que los entrenudos, hirsutas, verdes o con tintes violáceos, los márgenes pestañosos. *Lígulas* membranáceo-ciliadas, la porción membranacea de 0.5 mm de largo, cilias de 1.5 mm de largo; cuello piloso. *Láminas* linear-lanceoladas, de 12–30 cm de largo, 0.5–0.8 cm de ancho, erectas, ascendentes, planas, redondeadas en la base, el ápice atenuado, hirsutas, con pelos tuberculados, a esparcidamente pilosas, escabrosas, el nervio medio manifiesto. *Pedúnculos* subincluidos a exertos, hirsutos. *Inflorescencias* terminales exertas; panojas laxas, difusas, de 15–30 cm de largo, 10–12(–26) cm de ancho; *eje principal* anguloso, híspido hacia la base a glabro, escabriúsculo; ramificaciones de primer orden alternas a subopuestas, las inferiores ocasionalmente subverticiladas, de 8–18 cm de largo, divergentes, desnudas hacia la base, ramificaciones de segundo orden divergentes; espiguillas por rama 1–2(–3); pulvínulos cortamente pilosos; pedicelos de 2–20 mm de largo. *Espiguillas* solitarias, largamente ovoides, de 5–6.4 mm de largo, 1–1.2 mm de ancho, no estipitadas, pajizas, con tintes violáceos, glabras, la gluma superior y lemma inferior subiguales, superando 3.2–4 mm en largo al antecio superior. *Gluma inferior* de (2–)2.5–3 mm de largo, casi ½ del largo de la espiguilla, 5–7-nervia, aguda a obtusa. *Gluma superior* de 5–6 mm de largo, aguda, 10–13-nervia; gluma inferior y superior separadas por un conspicuo entrenudo ca. 0.4 mm de largo. *Lemma inferior* glumiforme, aguda, 10–12-nervia. *Pálea inferior* de 1.5–2 mm de largo, tan larga como el antecio superior, membranácea, los márgenes escabrosos. *Antecio superior* ovoide, de 1.6–2 mm de largo, 1–1.1 mm de ancho, liso, pajizo,

con tintes castaños a la madurez, lustroso, crustáceo, con 2 cicatrices basales, castañas a la madurez, ca. 0.2 mm de largo, lemma 5–7-nervia, pálea con papilas verrugosas en su ápice. *Cariopsis* de 1.5 mm de largo, 1 mm de ancho; hilo oblongo; embrión ½ a ¾ del largo de la cariopsis.

Distribución y ecología. Sur de los Estados Unidos de América y N de México (Fig. 5); crece en lugares abiertos sobre suelos arenosos; desde el nivel del mar hasta los 1000 m; florece y fructifica entre abril y diciembre.

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **Texas**: Frio Co., Dilly, 24 June 1941, *Tharp 43066* (MO); Kleberg Co., 2 mi. N of Riviera, off Hwy. 77, 15 Oct. 1946, *Lundell & Lundell 14683* (MO); 9 miles N of Raymondville, *Gould 11456* (US); El Toro Isla, al costado de la Laguna Madre, *Tharp 49042* (MO, US); Kingsville, *Piper s.n.** (US-558794); W of Kingsville, *Swallen 10254* (US); Norias Division, King Ranch, *Swallen 10197* (US); San Diego, *Croft 240* (US); 1 mile W of San Diego, *Gould 11000* (US). MEXICO. **Nuevo León**: Monterrey, *Hitchcock 5547** (US). **San Luis Potosí**: 10 km al S de Cárdenas, 1000 m, *Rzdewosky 4618* (US). **Tamaulipas**: Hacienda Buenavista, *Wooton s.n.** (US-1061806); Chamal, *Swallen 1642, 1693* *(US); sin localidad, 2 dic. 1930, *Viereck 857** (US).

Panicum capillarioides se distingue claramente del resto de las especies de la sección *Panicum* por poseer espiguillas largamente ovoides, con la gluma superior y la lemma inferior superando entre 3.2 y 4 mm al antecio superior.

7. **Panicum chasei** Rosengurtt, B. R. Arrillaga & Izaguirre, Bol. Fac. Agron. Univ. Montevideo 103: 9, fig. 2, 1968. TIPO: Uruguay. Rocha: Ruta 9, Fortaleza Santa Teresa, 3 feb. 1967, en costado del camino en suelo arenoso-arcilloso, *Rosengurtt 10804* (holótipo, MVFA no visto; isótipos, BAA, K, P, SI, US-2946507).

Plantas perennes, cespitosas, de 30–80 cm de alto. *Cañas* erguidas, simples, paucinodes; entrenudos cilíndricos de 3–13 cm de largo, cubiertos de pelos tuberculados tiesos a esparcidamente pilosos; nudos violáceos, pilosos, con pelos blanquecinos adpresos. *Vainas* de 3–12 cm de largo, usualmente menores que los entrenudos, cubiertas de pelos tuberculados. *Lígulas* membranáceo-pestañosas, de 0.7–1.8 mm de largo; cuello castaño claro, piloso. *Láminas* linear-lanceoladas, planas o con los bordes involutos, erectas, ascendentes, rígidas, de 9–25 cm de largo, 0.2–0.6 cm de ancho, angostadas en la base, con pelos tuberculados en ambas caras, más abundantes en la cara adaxial, el ápice acuminado, los bordes escabriúsculos, ciliados. *Pedúnculos* largamente exertos, cilíndricos, híspidos, de 10–31 cm de largo. *Inflorescencias* espiciformes a subespiciformes, de 8–24 cm de largo, 1–5 cm de ancho, con las ramificaciones adpresas al raquis, en ocasiones ligeramente divergentes; *eje principal* glabro, liso, anguloso; pulvínulos esparcidamente pilosos a glabros; ramificaciones alternas, las espiguillas adpresas sobre los ejes; pedicelos escabriúsculos, claviformes, de 1–5 mm de largo. *Espiguillas* anchamente ovoides, de 2.8–3.8 mm de largo, 1.1–1.5 mm de ancho, acuminadas, no estipitadas, glabras, pajizas y con tintes violáceos; gluma superior y lemma inferior subiguales, iguales o superando hasta en 0.3 mm al antecio superior. *Gluma inferior* de 1.5–2.4 mm de largo, ½ a ¾ del largo de la espiguilla, 5–7-nervia, nervio medio escabriúsculo, cortamente pubescente en la cara interna. *Gluma superior* de 2.8–3.5 mm de largo, 7–9-nervia, nervio medio escabriúsculo o no hacia el ápice, cortamente pilosa en la cara interna; estípite ausente. *Lemma inferior* de 2.7–3.5 mm de largo, glumiforme, 9-nervia. *Pálea inferior* elíptica, de 1.8–2.6 mm de largo, 0.9–1.2 mm de ancho, tan larga como el antecio superior, membranácea, finamente denticulada o no en los bordes superiores, con el ápice bilobado a entero. *Antecio superior* elipsoide, de 2–2.6 mm de largo, 1–1.3 mm de ancho, crustáceo, glabro, liso, lustroso, pajizo, castaño a grisáceo a la madurez, con dos cicatrices basales, de 0.15 mm de largo, castañas a la madurez; lemma superior 7-nervia, pálea superior con papilas simples en su ápice. *Cariopsis* elipsoide a ovoide, de 1.4–1.6 mm de largo, 0.8–1.1 mm de ancho; hilo punctiforme; embrión menos de la mitad del largo de la cariopsis.

Distribución y ecología. Argentina, Brasil y Uruguay (Fig. 9). Vive en campos; florece desde octubre hasta mayo.

Material adicional examinado. ARGENTINA. **Corrientes**: Estancia Rincón del Ambrosio, *Schwarz 9595* (LIL, LP). **Entre Rios**: Nueva Escocia, *Cordini 20* (BAA). BRASIL. **Rio Grande Do Sul**: Tupaceretán, *Rambo 9875** (US); Belem Velho, *Araujo 151* (BAA, US); Pelotas, *Araujo 527* (BAA); entre Cruz Alta y Panambí, 3 nov. 1962, *Rosengurtt & Del Puerto 8893** (BAA, SI, US); Porto Alegre, Morro da Gloria, *Valls 1646* (CEN); Fazenda Experimental de Criação Bagé, *Swallen 7467* (US). URUGUAY. **Rivera**: Subida de Pena, Sierra de la Aurora, *Rosengurtt B-7128* (US). **Salto**: San Antonio, *Orihuela 92* (US), *s.n.* (US-1648463). **Soriano**: Estación Juan Jackson, *Rosengurtt B-242* (US). **Tacuarembó**: Camino a Rivera, 32 km de Tacuarembó, 8 feb. 1981, *Cabrera & Zuloaga 32423**,** (SI, US).

Especie afín a *P. ghiesbreghtii* y *P. peladoense*. De la primera se separa por poseer panojas contraidas, espiguillas generalmente de mayor tamaño y por tener láminas menores. *Panicum peladoense*

difiere de *P. chasei* por sus panojas laxas, con espiguillas con antecio superior negro a la madurez y gluma superior caediza a la madurez de las espiguillas.

Panicum diffusum Sw., especie que crece en las Indias Occidentales, se diferencia de *P. chasei* por poseer laminas lineares hasta de 0.2 cm de ancho, panojas laxas y espiguillas menores, de 2–2.9 mm de largo por 0.8–1 mm de ancho, con pálea inferior reducida.

El ejemplar *Gallinal et al. 4473* se aparta de los restantes examinados por tener inflorescencias más laxas, con ramas divergentes del raquis.

8. Panicum decolorans Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 1: 100. 1816. TIPO: México. Querétaro: crescit in temperatis, apricis regni Mexicani prope Querétaro, alt. 995 hexap., *Humboldt s.n.*** (holótipo P, fragmento y foto, US-80663; isótipo, P).

Plantas anuales, cespitosas. *Cañas* erectas de (15–)30–90 cm de alto, geniculadas o no, simples o ramificadas en los nudos inferiores, paucinodes; entrenudos de 6–12 cm de largo, cilíndricos, huecos, glabros, hirsutos hacia la porción superior a glabrescentes; nudos cortamente pilosos. *Vainas* de 3.5–7 cm de largo, comúnmente más cortas que los entrenudos, hirsutas, con pelos tuberculados caducos, o glabras, los márgenes cortamente ciliados en toda su superficie o sólo hacia la porción superior, ocasionalmente con un margen ciliado y el restante glabro. *Lígulas* membranáceo-pestañosas, de 0.6–2 mm de largo; cuello glabro. *Láminas* lanceoladas, de 4.5–18 cm de largo, 0.5–1.5 cm de ancho, planas, de base redondeada y ápice agudo, glabras a hirsutas en la cara abaxial, ocasionalmente hirsutas en toda la superficie, con pelos tuberculados de 1–1.5 mm de largo, los márgenes basales ciliados con pelos caducos. *Pedúnculos* angulosos, hasta de 27 cm de largo, glabros a hirsutos hacia la porción superior. *Inflorescencias* terminales exertas, largamente pedunculadas, multifloras, espiciformes, de (5–)10–20 cm de largo, 0.5–1(–2) cm de ancho; *eje principal* anguloso, escabriúsculo; pulvínulos glabros; ramificaciones de primer orden adpresas al eje, ascendentes, en ocasiones la inferior algo divergente, alternas, con espiguillas congestas sobre ejes de tercer o cuarto orden; pedicelos claviformes, escabrosos, triquetros, de 1.5–4 mm de largo. *Espiguillas* largamente ovoides, de (4.2–)5–6 mm de largo, 1.8–2 mm de ancho, no estipitadas, glabras, pajizas, con tintes violáceos; gluma superior y lemma inferior subiguales o la gluma superior algo menor que la lemma inferior, 1–2 mm más largas que el antecio superior. *Gluma inferior* ovada, de 1.8–2.7 mm de largo, ½ o algo menor del largo de la espiguilla, aguda a obtusa, abrazando en la base a la gluma superior, 5–7-nervia, el nervio medio escabriúsculo. *Gluma superior* de (3.8–)5–5.9 mm de largo, aguda a acuminada, 10–13(–15)-nervia, la cara interna escabriúscula hacia el ápice. *Lemma inferior* glumiforme, 10–13-nervia. *Pálea inferior* reducida, de 1–1.5 mm de largo, ⅓ o menor del largo del antecio superior, membránacea, obtusa, glabra. *Antecio superior* ovoide, de 2.7–3.8 mm de largo por (1.1–)1.5 mm de ancho, glabro, pajizo a castaño, liso, lustroso, crustáceo, obtuso, fácilmente caedizo a la madurez antes de la caida de las glumas, la base con un anillo circular, castaño a la madurez; lemma 7-nervia; pálea con papilas verrugosas hacia el ápice. *Cariopsis* elipsoide, de 2–2.5 mm de largo por 1–1.5 mm de ancho; hilo oblongo; embrión ½ a ¾ del largo de la cariopsis.

Distribución y ecología. Endémica de México, crece en los estados de Baja California Sur, Chihuahua, Coahuila, Guanajuato, Hidalgo, Jalisco, Michoacán, Oaxaca, Puebla, Querétaro y San Luis Potosí (Fig. 6). En flor entre mayo y noviembre; llega hasta los 1870 m.

Material adicional examinado. MEXICO. **Chihuahua**: 10 km W of Carretas, 1675 m, 21 Aug. 1939, *Harvey 1578** (GH, US). **Coahuila**: Parras, 12 Nov. 1935, *Archer 3400* (US). **Guanajuato**: Estación El Chico, about 10 km east of Irapuato, *Sohns 210* (US). **Hidalgo**: Mun. Jacala, 4500 ft., mountain roadside, *Chase 7090** (ANSM, GH, MO, US), *7270** (GH, US). **Jalisco**: swampy ground beside Lake Chapala, near Tuxcueca, 4400 ft., 25 Aug. 1941, *Leavenworth & Leavenworth 1839* (F, MO, US); 1 mile E of Tuxpán, on Mex 15, 1870 m, 20 Oct. 1976, *Brunken & Perino 434* (MEXU, MO). **Michoacán**: Chavinda, *Hernández Xolocotzi et al. 2793* (US). **Oaxaca**: km 568 of Panamerican highway, *Baldwin Jr. 14321** (US). **Puebla**: Tehuacán, 5500 ft., 9 Aug. 1910, *Hitchcock 6057* (US). **Querétaro**: Querétaro, *Hitchcock 5822, 5864* (US), *Agniel & Arsène 10269** (US); on rocky slopes back of motel 5 miles N of Querétaro, 8 Sep., *Gould 11596** (US). **San Luis Potosí**: Cárdenas, *Hitchcock 5712* (F, GH, NY, US); 2 km E of Santa Catarina along hwy. 70, 1220 m, 23 Oct. 1978, *Reeder & Reeder 7042* (MEXU).

Afín a *P. parcum*, se distingue por los caracteres de la inflorescencia (laxa y difusa en *P. parcum*, de 6–15 cm de ancho), por poseer gluma inferior ½ o menos del largo de la espiguillá (¾ del largo en la última especie) y por carecer de un entrenudo marcado entre la gluma inferior y superior (mientras que *P. parcum* tiene un estípite ca. 0.6 mm de largo entre ambas glumas).

9. Panicum diffusum Swartz, Prodr.: 23. 1788. *Panicum diffusum* Sw. var. *genuinum* Döll in Martius, Fl. Bras. 2 (2): 199. 1877, nom. illeg. superfl. TIPO: Jamaica. "Jamaica, Hispaniola" (holótipo, S; fragmento y foto, US-76920; isótipos, G, M).

Panicum caespititum Lamarck, Tabl. Encycl. 1: 173. 1791. TIPO: "Ex Amer. merid. communic D. Richard" (holótipo, P, fragmento, US-2903511, foto US-76920).

Panicum diffusum Sw. var. *debile* Nees, Fl. Bras. Enum. Pl. 2: 172. 1829. *Panicum debile* Schult. Mantissa 2: 243. 1824, non *P. debile* Desf., 1798, non Ell., 1816, nec Poir., 1816. TIPO: "Hispaniola" (holótipo no visto, fragmento, US-974075).

Plantas perennes, cespitosas y cortamente rizomatosas. *Cañas* erguidas a decumbentes, algo geniculadas en la base, de (6–)15–60 cm de alto, ramificadas en los nudos medios o simples; entrenudos cilíndricos, huecos, cortamente pilosos a glabros; nudos corta a largamente pilosos. *Vainas* estriadas, de 2–6 cm de largo, glabras, los bordes membranáceos, cortamente pestañosos hacia la porción superior. *Lígulas* membranáceo-ciliadas, reducidas, de 0.6–1 mm de largo; cuello castaño, glabro. *Láminas* lineares, de (3–)6–15 cm de largo, 0.2 cm de ancho, patentes, los bordes involutos, aplanadas hacia la porción media, cara adaxial densamente pilosa con pelos blanquecinos, la cara abaxial glabra o esparcidamente pilosa, los márgenes basales con pelos tuberculados caedizos o sin lo mismos, el resto escabriúsculos, base angostada, el ápice subulado. *Pedúnculos* de 9–15 cm de largo, cilíndricos, glabros. *Inflorescencias* terminales exertas, laxas, difusas, de 3–16 cm de largo, 1.5–8 cm de ancho; *eje principal* anguloso, escabriúsculo; pulvínulos castaños, glabros; ramificaciones de primer orden alternas, raro opuestas, divergentes y distanciadas; ramas inferiores de 3–8 cm de largo, desnudas en su tercio inferior, con espiguillas congestas y adpresas, hacia la porción superior sobre los ejes de segundo orden; ejes de las ramificaciones y pedicelos triquetros, escabrosos. *Inflorescencias axilares* presentes, numerosas, similares a las inflorescencias terminales. *Espiguillas* largamente ovoides, de 2–2.9 mm de largo, 0.8–1 mm de ancho, no estipitadas, glabras, verdosas o con tintes violáceos, gluma superior y lemma inferior subiguales y superando 0.6–0.7 mm el largo del antecio superior. *Gluma inferior* de 1–1.2 mm de largo, ½ o poco menor del largo de la espiguilla, ovada, aguda, 5–7(–9)-nervia, con los nervios anastomosados hacia el ápice. *Gluma superior* de 2–2.8 mm de largo, 11–13-nervia, cortamente pilosa hacia el ápice en la cara interna. *Lemma inferior* de 2–2.8 mm de largo, 9–11-nervia, cortamente pilosa hacia el ápice en la cara interna. *Pálea inferior* ovada, reducida de 1–1.3 mm de largo, 0.6–0.8 mm de ancho, ½–¾ del largo del antecio superior, hialina, glabra. *Antecio superior* elipsoide, de 1.5–1.8 mm de largo, 0.6–0.8 mm de ancho, fácilmente caedizo a la madurez, pajizo, liso, lustroso, crustáceo, con dos cicatrices basales de 0.12 mm de largo; lemma 7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* de 1.1 mm de largo por 0.7 mm de ancho; hilo punctiforme; embrión menos de ½ del largo de la cariopsis.

Distribución y ecología. Se encuentra en las Indias Occidentales, en Bahamas, Cuba, Guadalupe, Jamaica, Martinica, Puerto Rico, República Dominicana y St. Thomas (Fig. 9). Llega hasta los 1500 m; en flor durante todo el año.

Material respresentativo citado. BAHAMAS. New Providence, Harold Road, *Britton & Brace 424* (NY, US). CUBA. Guanabacoa, *Hitchcock 23239* (US); Camaguey, sabana N of La Gloria, *Shaffer 385* (NY, US). **Habana**: Santiago de las Vegas, 17 Oct. 1904, *Van Hermann 355* (NY), *2444** (NY, US); near Santiago de Las Vegas, *Wilson 1405* (P, US); inter Campo Florido et Loma de Coca, 18 mayo 1914, *Ekman 995* (G, US). **Isla de la Juventud**: near Nueva Gerona, 12 May 1904, *Curtiss 494** (M, MO, NY, P, US); near Madruga, *Britton et al. 649* (NY). **Matanzas**: Sabanilla de La Palma, *León 9651* (NY). **Oriente**: Santiago de Cuba, in pastures N of the town, 26 June 1914, *Ekman 1517* (G, NY); Mir, in the savannas at the station, 22 Aug. 1916, *Ekman 7511* (G, US). **Pinar del Río**: Bahía Honda, among rocks in hillside, *Wilson 9443* (NY, US); near Guanajay, in grassy fields, *Palmer & Riley 802* (US). **Santa Clara**: Sagua, *Britton & Wilson 314* (NY); Santa Clara, *Britton et al. 6123* (NY). GUADALUPE. Grand-terre, *Richard s.n.* (P); sin localidad, *P. Duss 676* (P), *3181** (NY, US). HAITI. Vicinity of Bassin Bleu, 630–1500 m, *Leonard & Leonard 15090* (NY, US); vicinity of Mole St. Nicolas, on bare rocks, between bay and north coast of Cap du Môle, *Leonard & Leonard 13147* (US); montagnes du Iron d'Eau, between Source Matelas and Source Puantes, *Ekman 2151* (US). JAMAICA. Inverness, Lower Clarendon, 15 Oct. 1915, *Harris 12164** (MO, NY, P); Ewarton to Linstead, ditch in cut, *Hitchcock 9463* (US). MARTINICA. Coteaux des Trois Ilets, *Duss 536* (US). PUERTO RICO. Guanajibo, near Mayagüez, 11 Feb. 1915, *Britton & Cowell 4064* (MO, NY); Quebradillas, in pockets in limestone cliff above the sea, 22 Nov. 1913, *Chase 6577* (G, MO, NY, P, US). REPUBLICA DOMINICANA. **Santo Domingo**: vicinity of Ciudad Trujillo, *Allard 15744, 15902* (US); Azua, Valle de San Juan, 20 ago. 1929, *Ekman 13390* (G, NY). **Santiago**: Valle del Cibao, Hato del Yaque, *Ekman 16237* (US). **Monte Cristi**: foot of El Morro, near seashore, *Jiménez 3620* (US). ST. THOMAS. Northside Bay, Sep. 1880, *Eggers 76*** (G, M, MO, P, US).

Panicum diffusum se caracteriza por incluir plantas gráciles con cañas manifiestamente ramificadas, láminas linear-lanceoladas e inflorescencias con espiguillas adpresas en las ramas y espiguillas

de 2–2.9 mm de largo. Algunos especímenes de esta especie son glaucos y se asemejan a *P. filipes*, la que se distingue por el tipo de panoja y ancho y largo de la hoja y por el tamaño y forma de la espiguilla.

El material citado para Brasil por Doell (1877) como *P. diffusum* Sw. var. *subcontractum* corresponde a *P. exiguum* Mez. En esta obra Doell cita también un ejemplar de St. Bartholomei, *Forsstrom s.n.* (F, S), de las Antillas y que corresponde a *Panicum diffusum*. *Panicum diffusum* fue citada también para Brasil, basándose en la obra de Doell, por Beetle (1977) y Gould (1979).

Gould (1975, 1979), Waller (1976) y Beetle (1987) indican erróneamente que la especie crece en Texas, México y Brasil, sin citar ejemplares de herbario.

10. Panicum ephemeroides Zuloaga & Morrone, nom. nov. *Panicum ephemerum* Zuloaga, Morrone & Valls, Iheringia, Bot. 42: 4, fig. 1-8, 24 y 25. 1992, hom. illeg., non *P. ephemerum* Renvoize, 1979. TIPO: Brasil. Goiás: Mun. Jataí, 51 km a oeste do Rio Claro e 9 km a este do acesso a Perolândia ao longo da rodovia BR-364, 860 m, 3 abr. 1986, *Valls & Werneck 9867** (holótipo, CEN; isótipos, SI, US). Figura 19.

Plantas anuales, cespitosas, herbáceas, de 60–70 cm de alto. *Cañas* erectas, simples, paucinodes; entrenudos cilíndricos, huecos, glabros; nudos glabros. *Vainas* herbáceas, estriadas y con nervios anastomosados, glabras. *Lígulas* membranáceo-ciliadas, la porción membranácea de 0.4 mm de largo, cilias de 1.5–2.2 mm de largo. *Láminas* lineares, de 20–23 cm de largo, 0.2 cm de ancho, con los bordes involutos, la base redondeada y el ápice largamente atenuado, los bordes escabriúsculos. *Pedúnculos* de 15–25 cm de largo, cilíndricos, glabros. *Inflorescencias* terminales exertas, laxas, difusas, multifloras, ca. 30 cm de largo; *eje principal* anguloso, escabriúsculo a liso y glabro, con ramificaciones primarias divergentes del raquis, las inferiores alternas y las superiores opuestas a alternas; pulvínulos glabros y con tintes violáceos; ejes de las ramas escabrosos, con espiguillas adpresas a las ramificaciones secundarias, solitarias, distantes y cortamente pediceladas sobre ejes de tercer orden; pedicelos claviformes, escabrosos. *Inflorescencias axilares* numerosas, similares a las inflorescencias terminales. *Espiguillas* largamente elipsoides, de 3.5–3.6 mm de largo por 1.3 mm de ancho, biconvexas, no estipitadas, glabras, verdosas y con tintes violáceos, abiertas a la madurez, gluma superior y lemma inferior subiguales y de ápice violáceo largamente atenuado, superando 1 mm en largo al antecio superior. *Gluma inferior* de 2.8 mm de largo, ¾ del largo de la espiguilla, abrazadora, glabra, de ápice atenuado, 3(–5)-nervia, el nervio medio escabriusculo hacia el ápice. *Gluma superior* 5(–7)-nervia, el nervio medio escabriúsculo. *Lemma inferior* 5-nervia, glumiforme. *Pálea inferior* elíptica, de 2 mm de largo, 1 mm de ancho, tan larga como el antecio superior, hialina, los bordes escabriúsculos, glabra en el resto de su superficie. *Antecio superior* elipsoide, de 2.1 mm de largo, 1.1 mm de ancho, blanquecino, castaño a la madurez, crustáceo, lustroso, papiloso sobre el ápice de la pálea superior y con un anillo castaño en la zona de inserción con la raquilla; lemma 5-nervia; pálea con papilas verrugosas hacia el ápice. *Cariopsis* elipsoide, de 2.4 mm de largo, 1.6 mm de ancho, blanquecina; hilo oblongo; embrión ⅓ o menos del largo de la cariopsis.

Distribución y ecología. Conocida sólo por la colección típica en el estado de Goiás, Brasil (Fig. 8). Habita en campos, llegando hasta los 860 m; en flor en el mes de abril.

Especie relacionada a *P. stramineum*, de la que se distingue por tener esta última espiguillas dispuestas hacia el ápice de las ramificaciones, hallándose los ejes de las ramas desnudos hacia la porción inferior, espiguillas globosas de 2.3–3.2 mm de largo, gluma inferior ⅓–½ o un poco más del largo de la espiguilla y gluma superior y lemma inferior 9–11(–13)-nervias.

11. Panicum exiguum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. TIPO: Brasil. Minas Gerais: Serra de Caldas, *Mosen 4571* (holótipo, B, fragmentos, BAA, US-80623; isótipo, P). Figura 20.

Panicum diffusum Swartz var. *subcontractum* Döll in Martius, Fl. Bras. 2(2): 199. 1877. TIPO: Brasil. Minas Gerais: Guarda Mor, *Pohl 2435* (lectótipo, aquí designado, W).

Plantas anuales, cespitosas, de 10–30(–50) cm de alto. *Cañas* geniculadas, decumbentes, arraigadas o no en los nudos inferiores, luego erguidas a erectas, densamente ramificadas; entrenudos comprimidos, huecos, hirsutos, con pelos de base tuberculada a glabros, de 1.5–11 cm de largo; nudos pajizos a castaño-oscuros, densamente pilosos. *Vainas* de 1–4 cm de largo, comúnmente menores que los entrenudos, hirsutas, cubiertas de gruesos pelos tuberculados, los bordes pestañosos. *Lígulas* membranáceo-ciliadas, de 0.5–1.5 mm de largo, la porción membranosa reducida, luego largamente ciliadas; cuello pajizo, piloso. *Láminas* oblongo-

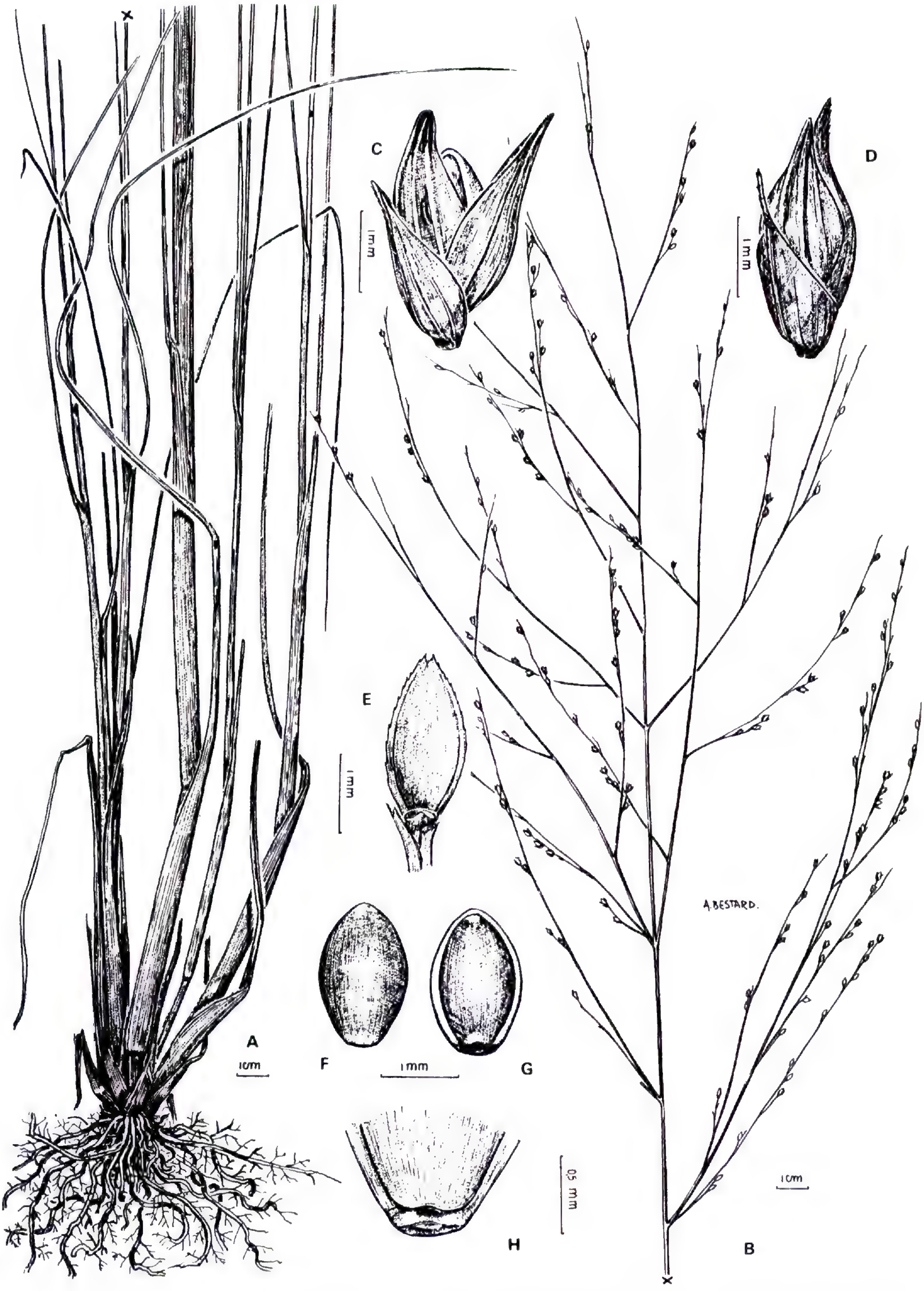


Figura 19. *Panicum ephemeroides.*—A. Hábito.—B. Inflorescencia.—C. Espiguilla, vista lateral.—D. Espiguilla vista del lado de la gluma inferior.—E. Pálea inferior.—F. Antecio superior vista del lado de la lemma.—G. Antecio superior visto de la pálea.—H. Base de la lemma y pálea superior. (*Valls & Werneck 9867.*)

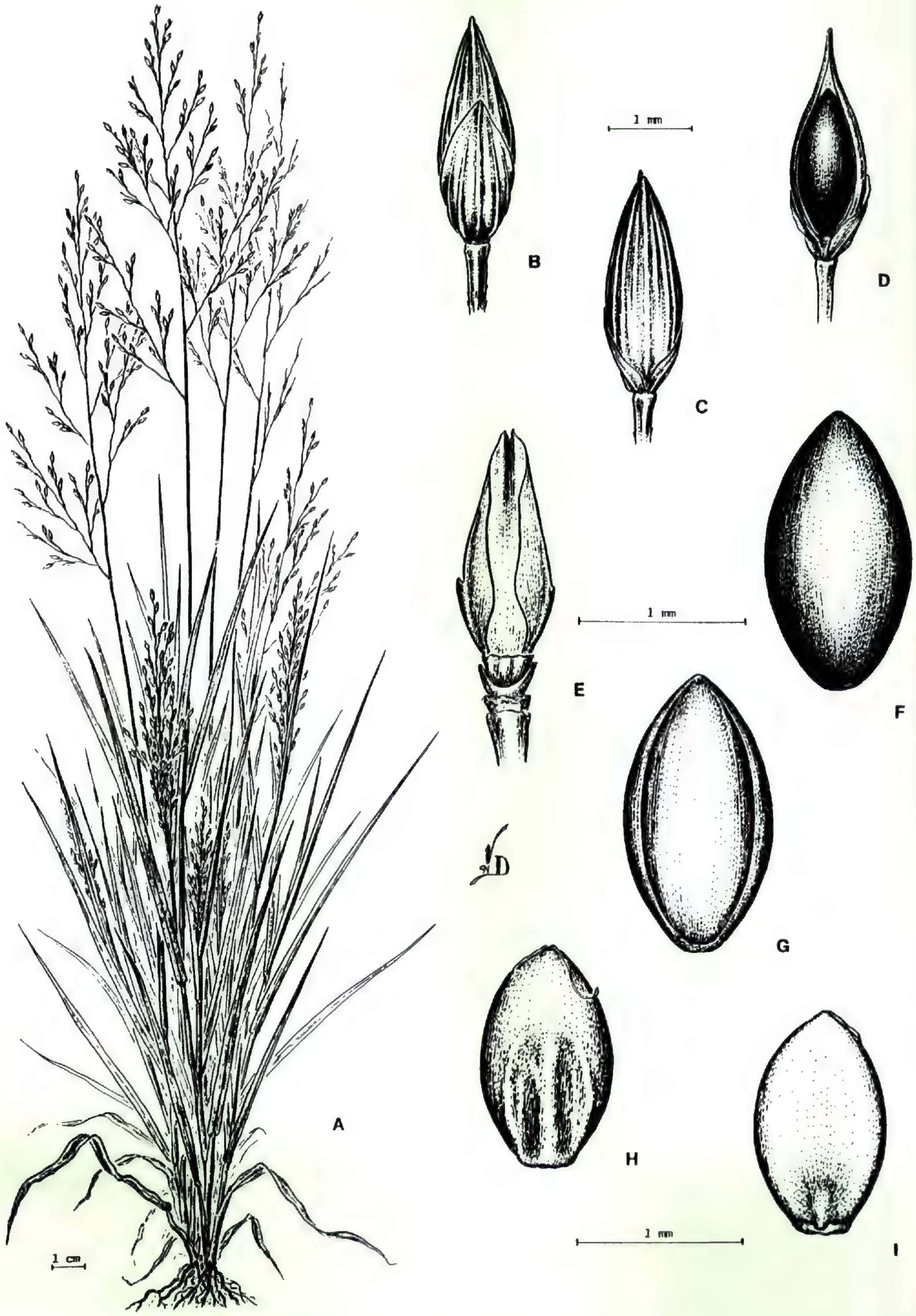


Figura 20. *Panicum exiguum.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Espiguilla sin la gluma superior, dejando al descubierto el antecio superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Cariopsis, vista escutelar.—I. Cariopsis, vista hilar. (*Valls et al. 7693.*)

lanceoladas a lanceoladas, acuminadas, de 2–6(–10) cm de largo, 0.2–0.4(–0.7) cm de ancho, planas, redondeadas a subcordadas en la base, con bordes escabriúsculos y largamente ciliados, cartilaginosos, el resto de la superficie hirsuta, con pelos tuberculados o sin los mismos. *Pedúnculos* subincluidos a exertos, hasta de 20 cm de largo, cilíndricos, hirsutos a glabrescentes. *Inflorescencias* laxas, difusas, piramidales, de 2.5–8(–14) cm de largo, 2–6(–8) cm de ancho, con espiguillas dispersas sobre las ramas, estas divergentes; *eje principal* anguloso, hirsuto, con largos pelos blanquecinos, a escabroso; pulvínulos glabros; ramificaciones alternas, raro opuestas, hirsutas a escabrosas, violáceas, pedicelos escabrosos, de 2–10 mm de largo, con largos pelos claviformes o sin los mismos. *Espiguillas* largamente ovoides, acuminadas, de (2.1–)2.6–3 mm de largo, 0.8–1 mm de ancho, abiertas a la madurez, no estipitadas, glabras, verdosas, con tintes violáceos; gluma superior y lemma subiguales y superando 0.6–1 mm en largo al antecio superior. *Gluma inferior* de (1.5–)1.7–2.4 mm de largo, ¾–⅘ del largo de la espiguilla, acuminada, (3–)5(–7)-nervia, el nervio medio escabroso hacia el ápice, cara interna escabriúscula hacia la porción superior. *Gluma superior* de 2.2–2.8 mm de largo, 7(–9)-nervia, el nervio medio escabroso hacia el ápice, este agudo a acuminado, la cara interna lisa a escabriúscula hacia el ápice, caediza y dejando a la vista el antecio superior negruzco; gluma inferior y superior separadas por un entrenudo ca. 0.3 mm de largo. *Lemma inferior* glumiforme, de 2.2–2.8 mm de largo, 7(–9)-nervia. *Pálea inferior* de (0.7–)1.2–1.6 mm de largo, 0.5–0.7 mm de ancho, ½–¾ del largo del antecio superior, ovada, pequeña, membranácea, glabra, bilobada o no en el ápice. *Antecio superior* elipsoide, de 1.4–1.8 mm de largo, 0.6–0.8 mm de ancho, liso, con papilas simples agrupadas en el ápice de la pálea, pajizo, negro a la madurez, caedizo antes que la gluma inferior y la lemma inferior, con dos cicatrices basales, de 0.1 mm de largo, castañas a la madurez; lemma superior 5–7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* de 1.1–1.4 mm de largo, 0.7–1 mm de ancho; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Su centro de distribución es Brasil, desde donde se extiende esporádicamente a Colombia, Venezuela, Bolivia, Perú, y Paraguay (Fig. 9). Llega hasta los 1000 m; habita en campos arenosos o arcillosos.

Nombre vulgar. "Capim do resfriado" (en el ejemplar *Macedo 2192*).

Material representativo citado. BOLIVIA. **Beni**: Estación Biológica de Beni, 40 km al este de San Borja, 14°50′S, 66°40′, 200 m, 15 abr. 1991, *Killeen 2834* (MO). **Santa Cruz**: Ñuflo de Chavez, San Antonio de Lomerio, 16°45′S, 61°48′W, 31 ene. 1985, *Killeen 823* (F, MO, SI). **Tarija**: Avilés, 6 km SW of Chocloca, *Beck 761* (K, LPB). BRASIL. **Ceará**: Sobral, *Black & Avelino 88C* (IAN). **Goiás**: Chapada dos Veadeiros, ca. 38 km N of Veadeiros, 1000 m, 16 Mar. 1969, *Irwin et al. 24519* (F, MO, K, NY, P, UB, US); Chapada dos Veadeiros, 4 km al S de Terezinha, *Anderson 7381** (MO, NY, UB); Santa Rita do Araguaia, *Chase 11791** (US). **Maranhão**: Carolina to San Antonio de Balsas, *Swallen 4106*** (K, US); Grajaú to Porto Franco, red clay outcrops, open ground, *Swallen 3822* (IAN, K, NY, RB, US); 100 m NE of main house of Fazenda "Morros," 35 km S of Loreto, 300 m, 3 Apr. 1962, *Eiten & Eiten 3956* (F, M, NY, SP, US). **Mato Grosso do Sul**: Campo Grande, sand and clay, 550 m, *Chase 10846* (F, GH, R, RB, US); Porto Esperanca, 28 Feb. 1930, *Chase 11071* (GH, IAN, RB). **Minas Gerais**: Corinto, Fazenda do Diamante, 600 m, 15 abr. 1931, *Mexía 5622** (BAA, F, G, GH, IAN, K, M, NY, P, R, US, W); Santa Terezinha, *Macedo 2194** (MO, US); Serra do Cipó, km 50, 800 m, 28 Mar. 1925, *Chase 9300** (F, GH, MO, NY, US). **Pará**: Estreito-Marabá, km I, *Pinheiro & Carvalho 55, 218, 483, 634* (UB, US); Transamazonian highway (BR-230), 6 km W of Estreito, Rio Tocantins, 6°32′S, 47°32′W, 300 m, 28 Feb. 1980, *Plowmann et al. 9269** (MO, SI). **Paraíba**: Campina Grande, *Pickel 3799* (IAN, RB, US). **Pernambuco**: Arcoverde, 21 jul. 1971, *Andrade Lima 71-6363* (F). **Piauí**: Gilbués, *Filgueiras & Rodrigues 1332* (CEN). **Rio Grande do Norte**: Santa Cruz, *Swallen 4859* (CEN, RB, SP). COLOMBIA. **Norte de Santander**: Los Estoaques, La Playa, 15 ene. 1974, *Balick 133* (COL). PARAGUAY. Río Apa, *Hassler 10986* (G, K, MO, NY, P, US). PERU. **Juniń**: Colonia Perené, 590 m, 22 Oct. 1923, *Hitchcock 22115** (F, GH, NY, R, US). VENEZUELA. **Aragua**: La Victoria, prope Colonia Tovar, *Fendler 2565* (K). **Distrito Federal**: Yaguara, hierba de 30–40 cm de alto, en sabanas altas de colinas, nov. 1940, *Tamayo 1469* (F, VEN). **Lara**: Dtto. Palavecino, dirt road between the quebrada "La Mata" and the east side of the Parque Nacional Terepaima, *Burandt Jr. & Gantaume V0498* (MO). **Trujillo**: south of Valera, stony flat above to río Matalán, 2600 m, 7 Mar. 1940, *Chase 12389* (NY, VEN).

Especie afin a *P. peladoense* Henrard, de la que se separa por ser una planta anual, con cañas decumbentes y manifiestamente ramificadas en la base, láminas de base redondeada a subcordada y espiguillas con la gluma inferior comúnmente ¾-⅘ del largo de la espiguilla. De *P. hirticaule* se distingue por ser la gluma superior caediza, antecio superior negruzco y gluma inferior ¾ a ⅘ del largo de la espiguilla.

El ejemplar *Swallen 4859* posee un porte mayor al que se presenta usualmente en esta especie, llegando hasta unos 90 cm de altura, con una inflorescencia de aproximadamente 20 cm de largo.

Luces (1963) citó el ejemplar *Tamayo 1469* como *Panicum hirticaule.*

12. Panicum flexile (Gattinger) Scribner in Kearney, Bull. Torrey Bot. Club. 20: 476. 1893. *Panicum capillare* L. var. *flexile* Gatt., Tennessee Fl.: 94. 1887. *Chasea flexilis* (Gatt.) Nieuwl., Amer. Midl. Naturalist 2: 65. 1911. TIPO: Estados Unidos de América. Tennessee: Cedar Glade near Nashville, Sep. 1888, *Gattinger s.n.* (lectótipo, designado por Hitchcock & Chase (1910) TENN, no visto, fragmento US-80552).

Plantas anuales, cespitosas, erectas, de 10–70 cm de alto. *Cañas* delicadas, erectas, paucinodes, ramificadas en los nudos inferiores; entrenudos de 3–9 cm de largo, 1 mm diám., surcados, glabros a hirsutos junto a la porción superior; nudos densamente pilosos, con pelos blanquecinos. *Vainas* de 3–6 cm de largo, usualmente más largas que los entrenudos, verdes a violáceas, híspidas, con los bordes esparcidamente pilosos. *Lígulas* membranáceo-pestañosas, de 0.6–1 mm de largo; cuello glabro, blanquecino. *Láminas* linear-lanceoladas, de (2.5–)7–25 cm de largo, 0.1–0.5 cm de ancho, planas o con los bordes involutos, ascendentes, erectas, predominantemente basales, verdes o con tintes violáceos, de base angosta y ápice agudo, con los bordes escabriúsculos, los basales largamente pestañosos, con pelos blanquecinos, tuberculados hasta de 5 mm de largo. *Pedúnculos* largamente exertos, hasta de 20 cm de largo. *Inflorescencias* terminales angostamente elipsoides, de 5–30 cm de largo, 1–6(–10) cm de ancho, difusas; *eje principal* glabro, liso, cilíndrico; pulvínulos glabros; ramificaciones de primer orden ascendentes, poco divergentes, alternas a subopuestas, ocasionalmente subverticiladas, glabras, lisas; ramificaciones de segundo orden, divergentes, laxas, difusas, con espiguillas aisladas, divergentes; pedicelos de 0.5–17 mm de largo, glabros, escabriúsculos. *Inflorescencias axilares* similares a las terminales, de menor tamaño. *Espiguillas* largamente elipsoides, de 2.4–3.6 mm de largo, 0.6–0.8 mm de ancho, no estipitadas, glabras, verdosas, con tintes cobrizos, de ápice largamente agudo; gluma superior y lemma inferior subiguales, superando 0.8–1.5 mm en largo al antecio superior. *Gluma inferior* ovado-acuminada, de 0.8–1.3 mm de largo, $\frac{1}{3}$–$\frac{1}{2}$ del largo de la espiguilla, 3-nervia. *Gluma superior* de 2.3–3.3 mm de largo, 7–9-nervia. *Lemma inferior* gluminforme, de 2.4–2.7 mm de largo, 7–9-nervia. *Pálea inferior* ausente. *Antecio superior* largamente elipsoide, de 1.6–1.7 mm de largo, 0.6 mm de ancho, crustáceo, liso, lustroso, brillante, pajizo y con tintes negruzcos a la madurez, con un anillo basal circular; lemma 7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* fusiforme, de 1.2 mm de largo, 0.4 mm de ancho, pajiza; hilo punctiforme; embrión $\frac{1}{2}$ del largo de la cariopsis.

Distribución y ecología. Se encuentra en Canadá y en los Estados Unidos de América (Fig. 10), en planicies, sobre suelos frecuentemente húmedos, o en ambientes rocosos. Llega hasta los 200 m; en flor entre agosto y octubre.

Material representativo citado. CANADA. **Ontario**: St. Clair River, 17 Aug. 1904, *Dodge 124* (US). ESTADOS UNIDOS DE AMERICA. **Alabama**: Franklin Co., E of Isball, 21 Sep. 1939, *Harper 3759** (MO, US). **Arkansas**: Marion Co., 600 ft, 7 Oct. 1950, *Demaree 30200* (US); Fulton, 16 Oct. 1901, *Bush 1087* (MO). **Georgia**: Catoosa Co., 1.9 mi E 18°N of Ft. Oglethorpe, 700 ft, 13 Sep. 1951, *Duncan 13221* (US). **Illinois**: Chicago, Lake Michigan, 14 Sep. 1900, *Chase 1473, 1474, 1479* (US). **Indiana**: SW of Griffith, 21 Aug. 1925, *Deann 42277** (US). **Kentucky**: Boone Creek, 28 Aug. 1926, *Anderson 358* (MO). **Michigan**: Huron Co., Port Crescent State Park day use area, entrance on Hwy. M-25, 1.6 mi. S and W of Port Crescent Rd., 9 Aug. 1982, *Gereau 1044* (MO). **Mississippi**: near Starkville, Sep. 1929, *Kearney Jr. 72* (US). **Missouri**: Ste. Genevieve Co., Establishment Creek, 22 Sep. 1976, *Christ 19* (MO). **New York**: Jefferson Co., SW of Chaumont, 27 Aug. 1923, *Fernald et al. 141415* (US). **North Dakota**: Benson Co., Wood Lake, Tokio, 1 Aug. 1940, *Stevens 477* (MO). **Ohio**: Cincinnati, Cox Bend of South York, 5 Sep. 1939, *Braum 2648* (US). **Oklahoma**: Muskogee Co., 25 Sep. 1940, *Bebb 5957a* (US). **Pennsylvania**: Lancaster Co., Diverville Swamp, Sep. 1892, *Small s.n.* (US-742109, 742110); Lancaster Co., Diverville Swamp, 2 Sep. 1862, *Porter s.n.* (US-952823). **Tennessee**: Maury Co., ca. 2.5 mi. SE Columbia by Tenn 50, 27 Aug. 1973, *Kral 51473* (MO); Johnson City, *Canby 221* (US). **Texas**: Clarksville, Feb. 1894, *Plank 10* pr.p. (US). **Virginia**: Rockbridge Co., about Lexington, 3 Sep. 1924, *Churchill s.n.* (MO-1056628); Fauquier Co., WW slope of Bull Run Mountains, 13 Sep. 1942, *Allard 10422* (MO).

Esta especie se caracteriza por poseer cañas floríferas que alcanzan ½ o más (hasta ¾) del alto de las cañas vegetativas. Las panojas son angostas y las espiguillas largamente elipsoides, con pálea inferior ausente y antecio superior con la base redondeada. Es frecuente observar que las plantas tengan en general tintes violáceos. Las inflorescencias axilares se encuentran incluidas en las hojas o son poco exertas.

Los ejemplares examinados de Canadá poseen pedicelos de 0.8 a 1.5 mm de largo, mientras que en los especímenes de los Estados Unidos los pedicelos llegan a tener 5 mm de largo.

13. Panicum furvum Swallen, Contr. U.S. Natl. Herb. 29: 416. 1950; emend. Davidse, Flora Mesoamericana 6: 306. 1994. TIPO: Guatemala. Huehuetenango: between Nentón and Las Palmas, vía Yalisjao, Rincón Chiquite, Chiaquial, Guaxacana, in Sierra de los Cuchumatanes, 30 Aug. 1942, 800–1200 m, *Steyer-*

mark 51627,*** (holótipo, US-1935086; isótipos, F-1202588, US-1935080).

Plantas perennes, densamente cespitosas. *Cañas* erectas de 16–20 cm de alto, simples, paucinodes; entrenudos de 2–3 cm de largo, papiloso-pilosos junto a la porción superior, luego glabros, pajizos o con tintes violáceos; nudos castaños, pilosos, con pelos blanquecinos ca. 1.5 mm de largo. *Vainas* de 2–3.5 cm de largo, usualmente más largas que los entrenudos, glabras a esparcidamente pilosas hacia la porción basal, pajizas o con tintes violáceos, los bordes membránaceos. *Lígulas* membranáceo-pestañosas, ca. 0.5 mm de largo; cuello glabro. *Láminas* linear-lanceoladas, de 2–12 cm de largo, 0.2–0.4 cm de ancho, erectas, ascendentes, predominantemente basales, planas o con los bordes involutos, glabras a esparcidamente pilosas en la cara adaxial, de base atenuada y ápice agudo, los bordes inferiores largamente pestañosos. *Pedúnculos* exertos, hasta de 9 cm de largo, cilíndricos, delgados, glabros a esparcidamente pilosos. *Inflorescencias* largamente exertas, laxas, paucifloras, de 3–6 cm de largo, 0.5–1.3 cm de ancho; *eje principal* glabro a esparcidamente piloso junto a la base; pulvínulos glabros; ramificaciones ascendentes, poco divergentes, glabras, lisas a finamente escabriúsculas, pajizas y con tintes violáceos, las inferiores hasta de 3 cm de largo; pedicelos claviformes, hasta de 7 mm de largo, adpresos, glabros. *Espiguillas* elipsoides, de 2.4–2.7 mm de largo, 0.8 mm ancho, de ápice largamente agudo, no estipitadas, glabras, pajizas, con el ápice de las brácteas violáceos; gluma superior y lemma inferior subiguales, superando 0.5–0.8 mm en largo al antecio superior. *Gluma inferior* ovado-acuminada, de 1.4–1.6 mm de largo, ½ o un poco más del largo de la espiguilla, 5-nervia, con el nervio escabriúsculo hacia el ápice. *Gluma superior* de 2.4–2.5 mm de largo, 7-nervia, caediza a la madurez, dejando el dorso del antecio superior descubierto, la cara interna escabriúscula hacia el ápice; gluma inferior y superior separadas por un breve entrenudo de la raquilla de 0.2 mm de largo. *Lemma inferior* glumiforme, de 2.4–2.6 mm de largo, 9-nervia, con la cara interna escabriúscula hacia el ápice. *Pálea inferior* reducida, lanceolada, de 1.2–1.4 mm de largo, 0.5 mm de ancho, ¾ del largo del antecio superior, hialina, glabra, de ápice bilobado, los bordes glabros a denticulados. *Antecio superior* elipsoide, de 1.6 mm de largo, 0.7 mm de ancho, crustáceo, liso, lustroso, glabro, negruzco a la madurez, con dos pequeñas cicatrices inconspicuas ca 0.1 mm de largo en la base; lemma 7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* no vista.

Distribución y ecología. Conocida sólo para la localidad típica en Guatemala (Fig. 9), creciendo en laderas de montaña entre los 800 y 1200 m.

Swallen (1950) señala, al describir la especie, que la espiguilla tiene 1.5–1.6 mm de largo. Sin embargo, el análisis del material típico permitió confirmar lo establecido por Davidse (1994), en el sentido de que la longitud de las espiguillas varía entre 2.4 y 2.7 mm.

Panicum furvum se relaciona, dentro del grupo de especies perennes con antecio superior negruzco y gluma superior caediza, a *P. peladoense*, especie sudamericana de la que únicamente se distingue por el tamaño de las plantas y espiguilla. Dentro de las especies centroamericanas se aproxima a *P. hallii* var. *hallii*, especie que tiene láminas rizadas en la base de las plantas, espiguillas mayores, de 2.7–4 mm de largo, con gluma superior persistente y antecio superior pajizo (o castaño a la madurez). Davidse (1994) indica la relación de *P. furvum* con especies subamericanas de la sección y menciona que, si bien su presencia en Guatemala es peculiar, no hay indicaciones en la etiqueta de colección del ejemplar tipo que indique que se trata de una especie introducida.

14. Panicum ghiesbreghtii E. Fournier, Mexic. Pl. 2: 29. 1886; E. Fourn. in Hemsl., Biol. Centr.-Amer., Bot. 3: 489. 1885, nom. nud. TIPO: México. "Absque loco," *Ghiesbreght s.n.* (lectótipo, designado por Hitchcock & Chase (1910), P, fragmento y foto, US-76924).

Panicum hirtivaginum Hitchcock, Contr. U.S. Natl. Herb. 12: 223. 1909. TIPO: Cuba: sin localidad, 1865, *Wright 758* (holótipo, US-559958; isótipos, MO, NY, P, US-823614, 974804).

Plantas perennes, cespitosas, de 40–90(–120) cm de alto, con innovaciones intravaginales. *Cañas* simples a ramificadas en los nudos inferiores, erectas; entrenudos cilíndricos, de 6–20 cm de largo, 2–3 mm diám., papiloso-pilosos, paucinodes; nudos densamente pilosos, con pelos blanquecinos. *Vainas* de 5–15 cm de largo, las inferiores comúnmente menores que los entrenudos, hirsutas con densos pelos tuberculados. *Lígulas* membranáceo-ciliadas, de (0.5–)1.5–2 mm de largo, con largos pelos por detrás en la base de la lámina; cuello densamente piloso. *Láminas* linear-lanceoladas, de 16–30(–55) cm de largo, (0.5–)0.8–1.4 cm de ancho, planas, erectas, ascendentes, de ápice largamente atenuado y base redondeada, la cara adaxial densamente pilosa, pilosidad serícea, cara abaxial hirsuta, con pelos tuberculados, los bordes inferiores ciliados, el nervio medio manifiesto. *Pedún-*

culos subincluidos en las vainas foliares a exertos, hasta de 40 cm de largo, glabros a hirsutos. *Inflorescencias* terminales laxas, amplias, multifloras, cortamente exertas a parcialmente incluidas, de 7–35 cm de largo, 5–23 cm de ancho; *eje principal* anguloso, escabroso; pulvínulos glabros; ramificaciones inferiores alternas, las subsiguientes verticiladas a opuestas o alternas, divergentes, ramificaciones de primer orden desnudas en su tercio inferior, las espiguillas apareadas sobre ejes de tercer orden hacia la parte superior, no congestas; pedicelos claviformes, escabrosos. *Inflorescencias axilares* presentes, similares a las inflorescencias terminales. *Espiguillas* largamente ovoides, de 2.6–3.1 mm de largo, 0.9–1.2 mm de ancho, no estipitadas, glabras, verdosas, con tintes violáceos, abiertas a la madurez; gluma superior y lemma inferior subiguales, superando 0.7–0.9 mm en largo al antecio superior. *Gluma inferior* de 1.4–1.7 mm de largo, ½ o poco menos del largo de la espiguilla, 5–7-nervia, nervio medio escabriúsculo hacia la porción superior, los nervios anastomosados hacia el ápice, el ápice agudo. *Gluma superior* de 2.5–3 mm de largo, 9–13-nervia, el nervio medio escabriúsculo hacia la porción superior, aguda, cortamente pilosa hacia el ápice en la cara interna. *Lemma inferior* de 2.5–3 mm de largo, 9–11-nervia, nervio medio escabriúsculo hacia la porción superior, aguda, cortamente pilosa hacia el ápice en la cara interna. *Pálea inferior* reducida, de 0.5–1.3 mm de largo, 0.5–0.8 mm de ancho, hialina, ⅓–½ del largo antecio superior, ovada, de ápice obtuso. *Antecio superior* ovoide, de 1.7–2.3 mm de largo, 0.8–1.1 mm de ancho, ¾ del largo de la gluma superior y lemma inferior, pajizo, liso, lustroso, glabro, crustáceo, el ápice obtuso, con 2 cicatrices basales, de 0.12 mm de largo, castañas a la madurez; lemma 7-nervia; pálea con papilas simples y micropelos globosos hacia el ápice. *Cariopsis* elipsoide, de 1.2–1.3 mm de largo, 0.7–0.8 mm de ancho; hilo oblongo; embrión ½ del largo de la cariopsis.

Distribución y ecología. Habita desde Estados Unidos, las Indias Occidentales y América Central hasta el norte de América del Sur, en Colombia y Venezuela (Fig. 6); crece en campos. Llega hasta los 2400 m. Florece y fructifica entre enero y noviembre.

Material representativo citado. ANTIGUA. Sin localidad, *Hitchcock 16382* (US), *Wullschagel 621, 622* (M); Scott's Hill Expt. Station, *Box 49* (US). BAHAMAS. Crooked Island, Sandrail Point, *Brace 4812* (NY, US). BELICE. **Corozal**: between Sarteneja and Chunox, 18°17′N, 88°15′W, 10 m, 18 Mar. 1987, *Davidse & Brant 32638** (MO, SI). COLOMBIA. **Magdalena**: Santa Marta, *Smith 165* (F, G, GH, K, MO, NY, P, US). **Santander**: Santander, Zapatoca, *Fassett 25492* (COL, US). **Tolima**: El Gigante, above Tolima, 500–1200 m, *Lehmann 8745* (NY, US). COSTA RICA. **Guanacaste**: along road W of the Cañas cemetery, 70 m, 24 June 1968, *Pohl & Davidse 10556* (F, MO, US). **San José**: San José, 1100 m, *Hitchcock 8452* (US), *Jiménez 530*** (US); Hacienda Taboga, *Jiménez 730* (US). CUBA. **Habana**: Calvario, Finca Santa Teresa, *León 2674* (P, US); cercanías de Madruga, *Britton et al. 745* (NY). **Holguín**: valle del Río Matamoros, cerca de Holguín al sur, *Suazer 1361* (NY). **Isla de la Juventud**: Santa Bárbara, Westport, *Ekman 12036* (G). **Matanzas**: cercanías de Coliseo, *León 8834* (NY). **Pinar del Río**: Herradura, *Tracy 9116* (NY); vicinity of Herradura, *Britton et al. 6349* (NY); Bahía Honda, between Gerardo and Corojalito, on the railroad track, *Ekman 12686* (US). **Santiago de Cuba**: Bayate, *Ekman 2011* (G), *9667* (NY); Guaro, 20 km from Preston, *Hitchcock 23397* (US). **Villa Clara**: Placetas del Sur, *León 6429* (US). DOMINICANA. **Distrito Nacional**: vicinity of Ciudad Trujillo, *Allard 14148* (US). **Santiago**: Valle del Cibao, Hato del Yaque, *Ekman 16129* (US). ECUADOR. Chacao, Miranda, 28 ago. 1939, *Eggers 14949* (F). **Manabí:** El Recreo, *Eggers 15419** (F, K, M, NY, P, US). EL SALVADOR. Acajutla, near sea level, 29 Nov. 1911, *Hitchcock 8993* (SI, US). ESTADOS UNIDOS DE AMERICA. **Texas**: Brownsville, 13 Oct. 1941, *Silveus 7293* (US). GUADALUPE. Sin localidad, *Questel 1439* (P, US); Basse Terre, *Duss 668* (P). HAITÍ. Vicinity of Pilate, 325 m, *Leonard 9607* (NY, US); vicinity of Pétionville, 15 June 1920, *Leonard 4901** (US); vicinity of Port au Prince, *Leonard & Leonard 15754* (US). HONDURAS. **Francisco Morazán:** El Zamorano, 800 m, 2 jul. 1947, *Molina 242* (F, GH, MEXU, MO); vicinity of El Zamorano, *Swallen 11147* (MO, US). JAMAICA. Inverness, Lower Clarendon, 22 Nov. 1913, *Harris 11691* (MO, NY, P, US). MEXICO. **Campeche**: 3 km al S de Bolonchen de Rejón, cerca de las Grutas de Xtacumbilxunan, por la carretera vía ruinas a Campeche, 25 jul. 1986, *Cabrera 11739* (MO). **Chiapas**: ca 22 km SE of Teopisca along Highway 190 to Comitán, pine-oak forest, 2040 m, 11 Aug. 1975, *Davidse & Davidse 9492* (MO). **Mexico**: Peñón, 1700 m, 8 Oct. 1933, *Hinton 4413* (MO, US). **Michoacán:** about 12 mi. W of Quiroga in open pine-oak forest, 7000–9000 ft, *Sohns 791, 797* (US). **Morelos:** Oaxtepec, *Matuda s.n.* (MEXU-288916). **Oaxaca:** Oaxaca, *Hitchcock 6143* (US). **Puebla:** roadside along route 130, 2.7 mi. S of the Puebla-Veracruz state line, 20 May 1979, *Harriman & Jansen 15627* (CHAPA). **Quintana Roo**: Coba, in savanna, north of Lake Coba, June 1938, *Lundell & Lundell 7791* (F, MEXU, MO, US). **San Luis Potosí:** low ground along Río Tampaón, *Chase 7480* (GH, US). **Sinaloa:** Rancho de la Nacha, 25 millas W de Angostura, *Vera Santos 1832* (NY). **Tabasco**: Fracc. Los Reyes calle Las Palmas 1 km al W de la carretera Cárdenas-Huimanguillo, 4 ago. 1981, *Suárez 4* (MO). **Tamaulipas**: Chamal, *Swallen 1717* (US); along route 85, ca. 4–5 miles south of Ciudad Mante, 18 Feb. 1961, *King 3791* (F, US). **Veracruz**: Orizaba, *Hitchcock 6363, 6391* (US); environs de Veracruz, *Gouin 21* (P). **Yucatán:** Chichen Itzá, along roadside, *Lundell & Lundell 7427* (US). NICARAGUA. **Boaco**: near Río Tecolostote, 7.5 km S of Hwy. 7 at El Papayal, ca. 12°11′N, 85°40′W, 60 m, 27 June 1982, *Stevens 21647* (MO). **Carazo**: Jinotepe, 500 m, *Hitchcock 8687* (US). **Chinandega**: Corinto, near sea level, 10 Nov. 1911, *Hitchcock 8755* (SI, US). **Estelí:** km 163 on Hwy. 1, ca. 11.2 km N of entrance to Estelí, ca. 13°13′N, 86°23′W, 920 m, 19 mayo 1981, *Stevens 20198*

(MO); 16 km N de Esteli, 900 m, 6 jul. 1970, *Pohl & Davidse 12210* (F, MO). **Managua**: along new road from Hwy. 1 (N of San Jacinto entrance) to San Francisco del Carnicero, ca. 4.8 km W of hwy. 1, 16 Aug. 1978, *Stevens 10006* (MO). **Matagalpa**: Matagalpa, 23 jul. 1969, *Zelaya 2307* (MO). **Rivas**: San Juan del Sur, near sea level, *Hitchcock* 8601 (US). PANAMÁ. Ancon, *Killip 4100* (US); in the vicinity of Balboa, Canal Zone, near swamp, *Hitchcock 7997* (SI, US), *8014* (US). **Panamá**: Taboga island, Gulf of Panama, *Hitchcock 8065* (SI, US), *8094* (US). PUERTO RICO. Vicinity of Coamo Springs, *Chase 6547* (NY); vicinity of Cayey, road to Guayama, *Chase 6744* (US). ST. THOMAS. Virgin Islands, sin colector (P). VIRGIN ISLANDS. Tortola, *Fishlock 206* (NY). VENEZUELA. **Aragua**: en terrenos salinos de la Est. Exp. del Servicio Shell para el Agricultor, *Tamayo 3949* (VEN). **Distrito Federal**: Ingomar, Turmerito, *Chase 12607* (US); La Florida, near Caracas, 12 Mar. 1938, *Alston 5298* (F, NY, P, US). **Falcón:** Sierra de San Luis, arriba de Santa María, 1100 m, a lo largo de la carretera, *Wingfield 5913* (MO). **Guárico**: Carretera de Santa María de Ipire a El Socorro, 15 km antes de la última población, en desvío a Zaraza, 150 m, *Zuloaga et al. 4506** (SI, VEN). **Lara**: Cerca de Sicarigua, *Burkart 16870* (VEN). **Mérida**: Brecenio Hacienda, 23 miles SE of Mérida, *Reed 517** (NY, US, VEN). **Miranda**: Chacao, *Williams 12152** (F). **Portuguesa**: a 4 km al W de Guanare hacia Ciudad Barinas, 09°03′N, 69°48′W, 200 m, 4 ago. 1989, *Zuloaga & Ortíz 4300, 4301** (MO, SI). **Yaracuy**: Bureche, antes de Barquisimeto, 12 abr. 1946, *Burkart 16508* (SI).

Especie afín a *P. hirticaule*, de la que se separa por incluir la última especie plantas anuales, con cañas comúnmente decumbentes, hojas generalmente de menor tamaño, patentes, delgadas y de base subcordada.

Hitchcock (1927) cita esta especie para Bolivia con el ejemplar *Steinbach 6979*, el que corresponde a *P. quadriglume*.

Esta especie fue erróneamente citada para Sudamérica austral por Hitchcock (1936), Swallen (1943), Luces (1963), Palacios (1969), Adams (1972), Smith et al. (1982), y Longhi Wagner & Boldrini (1988); el material citado por estos autores corresponde a *P. chasei*.

15. Panicum hallii Vasey, Bull. Torrey Bot. Club. 11: 61. 1884. TIPO: Estados Unidos de América. Texas: sin localidad, *Hall 816*** (holótipo, US-76926; isótipo, NY).

Plantas perennes, cespitosas, glaucas. *Cañas* erectas de (10–)20–75 cm de alto, simples o ramificadas en la base, paucinodes; entrenudos de 1–11 cm de largo, cilíndricos, huecos, glabros, pajizos o con tintes violáceos; nudos pilosos, cubiertos de pelos blanquecinos cortos, o glabros. *Vainas* de 3–11 cm de largo, glabras a hirsutas, con pelos tuberculados caducos, los márgenes membranáceos, glabros a ciliados junto a la región ligular. *Lígulas* membranáceo-pestañosas, de 0.6–1.2 mm de largo, cuello glabro. *Láminas* linear-lanceoladas, de 4–23 cm de largo, (0.1)–0.2–0.5 cm de ancho, erectas, ascendentes, las basales rizadas, planas o con los bordes involutos, glaucas, glabras a esparcidamente hirsutas, de base redondeada a angostada, continuándose imperceptiblemente con la vaina, el ápice agudo, con los bordes cartilaginosos, escabriúsculos, los inferiores pestañosos, con pelos papilosos, blanquecinos, hasta de 3.5 mm de largo. *Pedúnculos* hasta de 40 cm de largo, cilíndricos, glabros, verdes o con tintes purpúreos. *Inflorescencias* terminales exertas, laxas, de 9–31 cm de largo, 3–15 cm de ancho; *eje principal* triquetro, glabro, pulvínulos glabros; ramificaciones de primer orden alternas, divergentes, glabras, lisas; ramificaciones de segundo orden divergentes o adpresas, con espiguillas dispersas a aproximadas, adpresas a divergentes; pedicelos de 1–15 mm de largo, triquetros, claviformes, glabros, escabriúsculos. *Espiguillas* largamente ovoides, acuminadas, de 2.1–4 mm de largo, 0.8–1 mm de ancho, no estipitadas, glabras, verdosas o con tintes violáceos; gluma superior y lemma inferior subiguales, 0.3–1.2 mm más largas que el antecio superior. *Gluma inferior* ovada, de 1.2–2.4 mm de largo, ½–¾ de largo de la espiguilla, de ápice agudo a acuminado, 3–5-nervia, con el nervio medio escabriúsculo hacia la porción superior. *Gluma superior* de 2–3.5 mm de largo, de ápice acuminado, 7–9(–11)-nervia, escabriúscula en la cara interna hacia la porción superior; gluma inferior y superior separadas por un corto entrenudo de 0.3 mm de largo. *Lemma inferior* glumiforme, de 1.8–3.7 mm de largo, 9–11-nervia. *Pálea inferior* reducida, de 0.8–1.5 mm de largo, 0.3–0.4 mm de ancho, ½–¾ del largo del antecio superior, membranácea, hialina, glabra, con los bordes denticulados. *Antecio superior* ovoide a elipsoide, de 1.5–2.4 mm de largo, 0.7–1.2 mm de ancho, crustáceo, liso, pajizo, con tintes negruzcos a la madurez, con 2 cicatrices basales de 0.2 mm de largo, castañas a la madurez; lemma 7-nervia; pálea con papilas simples en su ápice. *Cariopsis* ovoide, de 1.2–1.7 mm de largo, 0.6–1 mm de ancho, blanquecina; hilo punctiforme; embrión ½ del largo de la cariopsis.

15a. Panicum hallii var. hallii

Panicum virletii E. Fournier, Mexic. Pl. 2: 29. 1886. TIPO: México: sin localidad, *Virlet 1305* (lectótipo, aquí designado, P, fragmento, US-86967).

Láminas de 4–15 cm de largo, (0.1–)0.2–0.5 cm de ancho. *Inflorescencias* con espiguillas aproximadas, adpresas. *Espiguillas* de 2.7–4 mm de largo.

Gluma superior y *lemma inferior* 0.8–1.2 mm más largas que el antecio superior.

Distribución y ecología. Ampliamente distribuido en el sur de los Estados Unidos y en México (Fig. 7); crece en campos áridos sobre suelos rocosos, hasta los 1920 m; florece entre marzo y octubre.

Nombre vulgar. "Sacate colorado" (en el ejemplar *Wooton s.n.*).

Material representativo citado. ESTADOS UNIDOS DE AMERICA. **Arizona**: Santa Cruz Co., Patagonia, 21 Sep. 1908, *Hitchcock 3706* (US); Santa Rita Mts., Empire Ranch, 20 Oct. 1902, *Griffiths & Thornber 238* (US); 42 mi. N of Tucson, 4500 ft, 15 Aug. 1915, *Hitchcock 13255* (US). **Colorado**: 25 mi. S of Pitchett, SW Baca Co., 4000 ft., 11 July 1947, Harrington 3361 (US). **New Mexico**: Doña Ana Co., near Tortugas Mts., 1270–1400 m, 30 June 1911, *Standley 6441* (US); Cimarron Canyon, 21/24 Aug. 1903, *Griffiths 5004* (US); 20 miles S of Roswell, Aug. 1900, *Earle 302** (NY, US). **Oklahoma**: Cimarron Co., 3 mi. N of Kenton, 9 July 1947, *Rogers 4756* (US). **Texas**: Young Co., 13 mi. SE of Graham, 15 Aug. 1965, *Gould 11075a* (US); Franklin Mts., vicinity El Paso, 22/25 May 1912, *Chase 5900* (US); Kerrville, *Hitchcock 5293* (US); Big Spring, 25/30 Aug. 1915, *Hitchcock 13411* (US); Williamson Co., roadside S.H. 29, 15.3 mi. E of Burnet, 9 Sep. 1969, *Waller 2163* (MO). **Utah**: Beaver County, Red Knoll, east side Pine Valley, 3 Sep. 1934, *Hutchings & Stachmann s.n.* (US-1648084). MEXICO. **Aguascalientes**: 1.5 km a Real a Asientos, 22 Oct. 1965, *Atrupo 1723* (MEXU). **Chihuahua**: km 5 desviación a Nuevo Casas Grandes de carretera Cd. Juárez, 1600 m, 19 sep. 1955, *Hernández & Mathus N-1911* (US); Sta. Eulalia Mountains, ago. 1875, *Pringle 376** (F, GH, MO, NY, P, US); base of Cerro Campana, 79 km N of Chihuahua, 1620 m, 23 Aug. 1975, *Davidse & Davidse 10057* (MO). **Coahuila**: Monclova, in vicinity of Chulavista Hotel, 23 May 1965, *Gould 1187* (US); Municipio de Castaños, south of Castaños, Rancho Santa Teresa, *Wynd & Muller 174** (GH, MO, NY, US); Laguna de Jaco, *Johnston & Muller 1111** (GH); San Antonio de los Alamos, eastern base of the volcanic Sierra de San Antonio de los Alamos, *Johnston 8250* (US), *8250 a* (GH); Sierra de las Cruces, eastern foothills 8 mi. north of Santa Elena Mines, 7 Sep. 1940, *Johnston & Muller 1017** (F, GH, US); 2 miles NW of Frontera, Aug. 1938, *Johnson 7170** (GH). **Durango**: 24 miles NW of La Zarca, 6200 ft., *Soderstrom 819* (US); desert along Hwy. 40, 15 km SW of Pedriceña, 22 June 1964, *Mick & Roe 44* (US). **Hidalgo**: Mun. Jalapa, 500 ft., 1 July 1030, *Chase 7256* (US). **Nuevo Leon**: Galeana, Puerto México, carretera 57, 67 km al N de Saltillo, 1600 m, 25 ago. 1978, *Bernal & Cárdenas s.n.* (MEXU-271683); N of Sabinas, Hidalgo, 28 Aug. 1971, *Beetle 1061* (MO). **Oaxaca**: Mun. Zapotitlan, 4 km al E de Zapotitlan Salinas, 25 sep. 1990, *Sánchez-Ken et al. 328* (MEXU). **Puebla**: Afueras de Tehuacán, por la carretera a Esperanza, 1 sep. 1989, *Chiang et al. 294* (MEXU). **Querétaro:** 2 mi. S of Querétaro, 6400 ft., *Soderstrom 531* (US). **San Luis Potosí:** valley of the Rioverde between Rioverde and San Ciro, 850–1000 m, 12 Sep. 1954, *Sohns 1215* (US); Cárdenas, 19/20 July 1910, *Hitchcock 57191/2* (US); 10 km al W de Guadalcazar, 1600 m, *Rzedowsky 4931* (GH, US); Valle de Rioverde, between Rioverde and Boquilla, *Sohns 1248* (F, MEXU, P, US). **Tamaulipas**: vicinity of San Miguel, *Bartlett 10591* (GH); vicinity of Victoria, 320 m, *Palmer 554* (US); 35 km from Victoria on the road to Casas and Soto La Marina, ca. 280 m, 3 Oct. 1956, *Martínez Martínez & Borja Luyando F-2303* (MEXU, US). **Sin Estado**: sin localidad, *Virlet 1371* (US).

Existen especímenes considerados aquí dentro de la variedad típica que poseen características intermedias con la var. *filipes*, incluyendo plantas de mayor tamaño, con inflorescencias con ramificaciones abiertas, espiguillas de 2.9 mm de largo. Entre los mismos se pueden citar a *Waller 2434, Gould 7674, Reverchon 3527, Warnock s.n., Bush 858, Hall 817, Palmer 1338, Shreve & Tinkham 9897, Roybal 883, Sohns 1215, Rzedwosky 5174, Martínez Martínez & Borja Luyando F-2303.*

15b. Panicum hallii var. **filipes** (Scribner) F. R. Waller, Southw. Naturalist 19: 105. 1974. *Panicum filipes* Scribn., Bot. Explor. S. Texas 1: 13. 1895. TIPO: Estados Unidos de América. Texas: growing in rich shaded ground in the upper part of the "Arroyo" at Corpus Christi, 30 ft., 31 May 1894, *Heller 1809* (holótipo, US-2463136, fragmento y foto, US-953192; isótipo, NY).

Láminas de 11–23 cm de largo, 0.2–0.4 cm de ancho. *Inflorescencias* con espiguillas dispersas, no adpresas sobre las ramas. *Espiguillas* de 2.1–2.8 mm de largo. *Gluma superior* y *lemma inferior* 0.3–0.7 mm más largas que el antecio superior.

Distribución y *ecología.* Frecuente en campos y en bordes de caminos (Fig. 10). Florece entre marzo y diciembre.

Material representativo citado. ESTADOS UNIDOS DE AMERICA. **Texas**: San Patricio Co., near entrance to Lake Corpus Christi State Park, 2 Oct. 1964, *Gould 10972, 10973* (US); along Ennis Joslin Road by golf course, 0.9 mi. N of Padre Island Parkway, Corpus Christi, 22 July 1969, *Waller 2017* (MO). MEXICO. **Coahuila**: 24 km E of Don Martín Dam, 335 m, 20 mayo 1939, *Harvey 950* (US); El Berrendo, near Múzquiz, *Harvey 1186** (MO, US). **Nuevo Leon**: 12 mi. S of China on the road Foward Méndez, 7 Dec. 1960, *Crutchfield & Johnston 6068* (US); Pan-American Highway from Laredo to Monterrey, near Mamulique Pass, 1500 ft., *Leavenworth & Leavenworth 742* (F, MO). **San Luis Potosi**: El Banito, *Chase 7558** (GH). **Tamaulipas**: El Canelo Ranch, 24 mi. N of San Fernando on the Matamoros highway, 7 Dec. 1959, *Johnston 4870* (MEXU); Chamal, *Swallen 1716* (US); Hacienda Buena Vista, *Wooton s.n.* (US 1061807); Laredo, 28 ago. 1971, *Beetle et al. 1031* (MO).

Correll & Johnston (1970) citan a *P. filipes* como una especie afín a *P. halli*, de la que se distingue por el tamaño de la espiguilla (de 2–3 mm, panoja más amplia y láminas mayores en *P. filipes* y espiguillas de 3–3.7 mm en *P. halli*). Además rela-

ciona a la especie con *P. pilcomayense* (esta aparentemente introducida en Texas).

Se considera que el ejemplar *Johnston 4870,* citado por Waller & Morden (1983) bajo *P. tamaulipense,* pertenece a *P. hallii* var. *filipes.*

Existen, dentro del material considerado de esta variedad, ejemplares, como *Beetle et al. 1031, Waller 2008, Hitchcock 5500, Harvey 950,* que poseen características intermedias con la variedad típica, como el poseer espiguillas adpresas sobre las ramificaciones, siendo las medidas de las espiguillas coincidentes con el rango de variación existente en la variedad *filipes.*

Los ejemplares *Lundell & Lundell 10657, Swallen 1467* y *Swallen 1506* se caracterizan por poseer espiguillas menores y agrupadas en el extremo de las ramificaciones, hallándose la mayor parte de las ramas desnudas hacia la base.

16. Panicum hillmanii Chase, J. Wash. Acad. Sci. 14: 345. 1934. TIPO: Estados Unidos de América. Texas: Amarillo, 11 ago. 1918, *Hitchcock 16206* (holótipo, US-1037542).

Plantas anuales, cespitosas, de 15–40 cm de alto. *Cañas* erectas a geniculadas, arraigadas y ramificadas en los nudos inferiores; entrenudos de 3–5 cm de largo, hirsutos hacia la porción superior; nudos pilosos, contraidos, castaños. *Vainas* de 4–6 cm de largo, usualmente más largas que los entrenudos, verdosas o con tintes violáceos, densamente híspidas, con pelos papilosos, un borde pestañoso, el restante glabro. *Lígulas* membranáceo-pestañosas, de 1–2 mm de largo; cuello piloso. *Láminas* linear-lanceoladas, de 5–20 cm de largo, 0.4–1 cm de ancho, planas, ascendentes, erectas, híspidas a esparcidamente pilosas en la cara adaxial, de base subcordada a redondeada, el ápice agudo, márgenes escabriúsculos, largamente pestañosos hacia la base, con pelos papilosos, blanquecinos, hasta de 5 mm de largo. *Pedúnculos* subincluidos en las vainas foliares, densamente híspidos hacia la porción distal. *Inflorescencias* laxas, cortamente exertas, de 10–19 cm de largo, 10–18 cm de ancho; *eje principal* anguloso, escabriúsculo, densamente híspido hacia la base o en toda su extensión; pulvínulos híspidos; ramificaciones de primer orden alternas a subopuestas, las inferiores verticiladas, divergentes, ascendentes, escabriúsculas, esparcidamente pilosas hacia la base; ramificaciones de segundo orden divergentes, con espiguillas adpresas sobre los ejes; pedicelos escabriúsculos, adpresos, de 0.3–1 cm de largo. *Espiguillas* globosas, de 2.4–2.8 mm de largo, 1–1.1 mm de ancho, túrgidas, no estipitadas, pajizas o con tintes violáceos a ferrugíneas, glabras, de ápice acuminado; gluma superior y lemma inferior subiguales, tan largas como el antecio superior o superándolo hasta 0.4 mm. *Gluma inferior* aovada, de 1.2–1.6 mm de largo, ½ o un poco menor del largo de la espiguilla, de ápice acuminado, 3–5-nervia. *Gluma superior* de 2.4–2.7 mm de largo, 7–9-nervia, el nervio medio escabriúsculo hacia el ápice. *Lemma inferior* glumiforme, de 2.2–2.7 mm de largo, 9-nervia, el nervio medio escabriúsculo hacia el ápice. *Pálea inferior* lanceolada, de 1.2–1.5 mm de largo, 0.8 mm de ancho, ¾ del largo del antecio superior, glabra, hialina. *Antecio superior* elipsoide, de 1.8–2 mm de largo, 0.8–1 mm de ancho, crustáceo, pajizo, castaño oscuro a la madurez, liso, lustroso, con 2 cicatrices basales conspicuas, ca. 0.6 mm de largo, castañas a la madurez; lemma 7-nervia; pálea con papilas verrugosas junto al ápice. *Cariopsis* ovoide, de 1.6 mm de largo, 0.6 mm de ancho, pajiza a blanquecina; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Habita en los Estados Unidos de América, en los estados de California, Kansas, Oklahoma y Texas (Fig. 10). Crece en suelos arcillosos en praderas; frecuente en bordes de caminos. Florece y fructifica entre mayo y octubre.

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **California**: Solano Co., 3 mi. S of Purah Creek, road 31, 23 June 1969, *Rose 69039* (MO); Ventura Co., Maricopa Rd. (route 399) near Meiners Oaks, Ojai Valley, 5 Oct. 1963, *Pollard s.n.* (MO-1970993). **Kansas**: Ulysses, 27 June 1893, *Thompson 56* (US); Bucklin, 1892, *Hitchcock s.n.* (US-2434893); vicinity of Coldwater, along road 2 mi. W of town, 8 July 1929, *Rydberg & Imler 734* (MO). **Oklahoma**: along railroad near Snyder, 19 Sep. 1903, *Eggert s.n.* (MO-2974983); Frederick, 26 July 1903, *Ducan 100* (MO); Kingfisher Co., Huntsville, 25 May 1896, *Blankinship s.n.* (MO 2974984); Comanche Co., 1.8 mi. SE of Quanah Lake, Wichita Mountains Refuge, 21 July 1941, *McMurry 978* (US); Washita Co., near Bessie, 16 June 1913, *Stevens 962* (US); Washita or Swanson Co., *Stevens 1197* (US). **Texas**: Randall Co., Canyon, 2 June 1918, *Palmer 13885, 14078* (MO); Brewster Co., Kokernott Ranch, 8 mi. NE of Alpine, 27 July 1941, *Warnock 20925* (MO); Oklaonian, 31 May 1902, *Reverchon 2840* (MO); prairie near Stanton, 13 June 1900, *Eggert s.n.* (MO-2974990); Galveston, 23 Sep. 1901, *Tracy 7409* (MO); Nolan Co., Roscoe, 7 Sep. 1941, *Tharp s.n.* (MO-1275630); Rapton, Oct. 1925, *Kay 9180* (US); Abilene, 21 May 1902, *Tracy 8295*,*** (MO, US); sin localidad, 1889, *Nealley s.n.* (US-952982).

Especie afín a *P. stramineum* y *P. capillare.* De *P. stramineum* se separa por tener ramas inferiores de la inflorescencia verticiladas, eje principal y los pulvínulos de la inflorescencia híspidos, pálea inferior reducida, ¾ del largo del antecio superior, y cicatrices conspicuas en la base del antecio superior. De *P. capillare* se distingue por tener espi-

guillas globosas, acuminadas, con pálea inferior desarrollada, ¾ del largo del antecio superior y antecio superior con cicatrices conspicuas en su base.

Cabe destacar que en algunos especímenes, como por ejemplo en *Palmer 14078*, la gluma superior es caediza, dejando al descubierto el dorso de la lemma superior.

17. Panicum hirsutum Swartz, Fl. Ind. Occ. 1: 173. 1797. TIPO: Jamaica, *Swartz s.n.* (holótipo, S, fragmento y foto, US-76922). Figura 21.

Panicum chacoense Parodi, Darwiniana 15: 102, fig. 8. 1969. TIPO: Argentina. Chaco: Isla Brasilera, 19 ene. 1963, *Schulz 12138** (holótipo, BAA; isótipos, G, SI).

Plantas perennes, robustas, hasta de 3 m de alto, cortamente rizomatosas. *Cañas* multinodes, postradas, con raíces fulcrantes en los nudos inferiores, y erguidas en la extremidad, ramificadas en los nudos medios; entrenudos de 11–20 cm de largo, 0.4–0.8 cm diám., cilíndricos, huecos, pajizos, con pelos tuberculados urticantes, caducos; nudos contraidos, violáceos, pilosos. *Vainas* de 14–20 cm de largo, mayores o menores que los entrenudos, estriadas, hirsutas, con pelos urticantes caedizos y de base tuberculada, adpresos, verdosas o con tintes violáceos, de bordes membranáceos, glabros o con uno de los márgenes pestañoso. *Lígulas* membranáceas en la base y cortamente ciliadas en la porción superior, de 0.2–0.7 mm de largo, con largos pelos por detrás en la base de la lámina; cuello piloso. *Láminas* lanceoladas, de 20–50 cm de largo, 1.5–3.5 cm de ancho, planas o con los bordes involutos, de base subcordada a cordada, glabras o con escasos pelos esparcidos, el nervio medio manifiesto, los bordes escabriúsculos. *Pedúnculos* cilíndricos, hasta de 25 cm de largo, glabros. *Inflorescencias* terminales, laxas, contraidas a difusas, multifloras, de 25–45 cm de largo, 5–15 cm de ancho; *eje principal* anguloso, escabroso; pulvínulos levemente pilosos a glabros; ramificación inferior verticilada, las restantes opuestas o alternas, adpresas al raquis a divergentes, las espiguillas adpresas, cortamente pediceladas sobre las ramas; pedicelos de 0.5–2 mm de largo, escabrosos. *Espiguillas* angostamente ovoides, de 1.8–2.6 mm de largo, 0.5–0.9 mm de ancho, no estipitadas, glabras, pajizas, gluma superior y lemma inferior subiguales, tan largas como el antecio superior. *Gluma inferior* de 0.7–1.4 mm de largo, ovada, ½ de la longitud de la espiguilla o algo menor, 3–5-nervia, cortamente pilosa en el ápice de la cara interna o totalmente glabra. *Gluma superior* de 1.7–2.2 mm de largo, 7–11-nervia. *Lemma inferior* de 1.7–2.2 mm de largo, 7–9-nervia, glumiforme. *Pálea inferior* lanceolada, de 1.3–1.7 mm de largo, 0.3–0.4 mm de ancho, ¾ del largo del antecio superior, membranácea, hialina, con los bordes denticulados. *Antecio superior* angostamente elipsoide, de 1.2–1.6 mm de largo, 0.5–0.7 mm de ancho, glabro, liso, lustroso, pajizo, castaño a la madurez, con 2 cicatrices en la base de la lemma de 0.1 mm de largo, castañas a la madurez; pálea con papilas simples junto al ápice. *Cariopsis* elipsoide, de 0.8 mm de largo, 0.5 mm de ancho, pajiza; hilo punctiforme; embrión menos de la mitad del largo de la cariopsis.

Distribución y ecología. Originalmente descrita para Jamaica, crece en el sur de los Estados Unidos de América y México, hallándose abundantemente en Mesoamérica y las Indias Occidentales, habiendo sido hallada en mucha menor proporción en Sudamérica en Colombia, Venezuela, Ecuador, Perú, Brasil y la Argentina (Fig. 4). Habita en lugares húmedos a lo largo de cursos de agua o en bordes de pantanos, entre los 30 y 1800 m.

Nombre vulgar. "Cortadera," "gamelote" (en Venezuela, de acuerdo al ejemplar *Tamayo 1768*).

Material representativo citado. ANTIGUA. Donovans Bridge, *Box 176* (US). **Santa Lucia:** Mabouya Valley, *Box 190* (US). ARGENTINA. **Chaco**: Isla Brasilera, *Schulz 12349* (CEN, F). BELICE. **Cayo**: 9.5 miles S of Georgeville, on road to Agustine, 30 May 1973, *Croat 23483* (MO); vicinity of Millionario between the McCal River and Cuevas, 1900 ft., 30 May 1973, *Croat 23664* (F, MO); Central Farm, *Reyes 34* (US); Vaca Plateau, below Blue Hole Camp, 13 Aug. 1980, *Whitefoord 2090* (MO). **Orange Walk:** ½ mi. E of San Antonio, 8 Dec. 1976, *Leino 76105* (MO). **Stann Creek**: Humming Bird Highway, 13 Sep. 1954, *Gentle 8380* (F, G, MO, NY, US). **Toledo**: Pate's Camp, Edwards Road beyond Columbia, *Gentle 7120* (F, G, NY, US); Maya Mountains, canyon along Bladen Branch from Richardson Creek to Quebrada de Oro, 16°32′N, 88°46′49″W, 100–200 m, 12 Mar. 1987, *Davidse & Brant 32401* (MO). Sin localidad, *Smart 112* (F). BRASIL. **Pará**: Lower Amazon, Estate Cacanal Grande, *Goeldi 111, 128* (US). COLOMBIA. **Bolivar**: along the Caño Chacagua, N of Los Piñones, Island of Mompós, Lands of Loba, *Curran 261* (US); along the Mompós-Juana Sánchez trail, Island of Mompós, *Curran 250* (US); Canabetal, *Pennell 3866* (GH). **Cundinamarca**: La Mesa, 1200 m, *Triana s.n.* (US-1865276). **Magdalena**: alrededores de Ciénaga, *Romero Castañeda 8948* (MO, NY); Santa Marta, *Smith 164* (GH, K, MO, P, NY, US). **Santander**: Boca Sogamoso, Río Magdalena, 110 m, *Pennell 3849* (GH, NY, US); prope Billete Blanco, *Woronow et al. 4691* (US). Sin estado ni localidad, *Mutis 2151* (US). COSTA RICA. **Heredia**: Finca La Selva, 100 m, 21 abr. 1982, *Hammel 11795* (MO). **Limón**: near Puerto Limón, in plantations, *Pittier 3634* (NY, US); margin of Bonilla Lakes, above Tunnel Camp, 13 Dec. 1929, *Dodge et al. 5610* (MO).

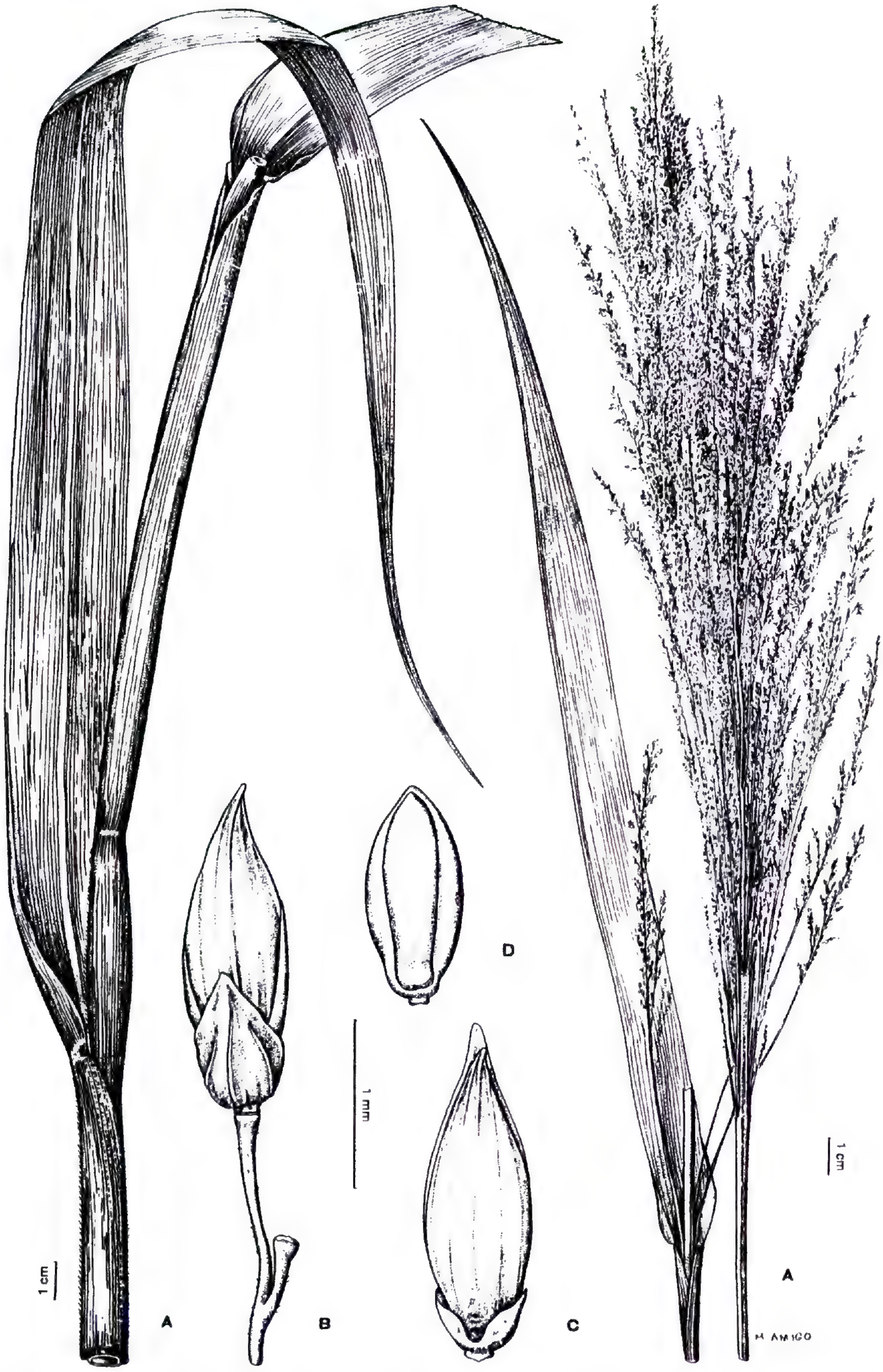


Figura 21. *Panicum hirsutum.*—A. Porción de una caña florífera.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Antecio superior visto de la pálea. (*Schulz 12138.*)

CUBA. **Cienfuegos**: Soledad, *Jack* 6295 (NY, US). **Habana**: Guanimas, on beach, 22 Aug. 1929, *León 14181* (MO, US). **Oriente**: Los Caños, S of Guantánamo, 7 Aug. 1913, *León 3913* (US); Bayate, near roads, *Ekman 6118, 6183, 10068* (US); Preston, on the railroad, 13 Nov. 1914, *Ekman 3419* (NY, US). **Pinar del Río**: Mangas, Pueblo Nuevo, Hato del Corojal, 9 Oct. 1923, *Ekman 17578* (US). **Villa Clara**: Caibarién, *Ekman 16312* (US); Cienaguita, *Combs 259* (NY). DOMINICANA. **Barahona**: valley of Neiba, *Howard 8357* (US); Barahona, Río Yaque del Sur, *Ekman 5791* (US). **Duarte**: valle del Cibao, Pimentel, at Río Cuaba, *Ekman 13275* (US). **Samana**: Sánchez, *Jiménez 4309* (US). ECUADOR. **Guayas**: Panigón Plantation, 8 miles S of Milagro, 50 m, *Hitchcock 20580* (GH,

NY, US), *20601* (US). ESTADOS UNIDOS DE AMERICA. **Texas**: Cameron Co., vicinity of Brownsville, 1 Aug. 1921, *Ferris & Duncan 3175* (MO, US); Cameron Co., Southmost, 1941, *Davis s.n.* (MO-1273655); Río Rico, near Río Grande, about 6 miles from Mercedes, *Silveus 625* (US); Brownsville, 18 Apr. 1917, *Nelson s.n.* (US). GUADALUPE. Entre la Riviere-Salée et St. Lucie, *Duss 768* (NY); sin localidad, 1897, *Duss 3917* (MO, NY, US), *L'Herminier s.n.* (G). GUATEMALA. **Huehuetenango**: vicinity of Ixcan, Sierra de los Cuchumatanes, 24 July 1942, *Steyermark 49430* (F). **Izabal**: Finca Murciélago, ca. 10 miles E of El Estor on Lake Izabal, 13 Sep. 1961, *Popenoe 34* (F); seashore around Punta Palma, across bay from Puerto Barrios, 22 Apr. 1940, *Steyermark 39802* (F). **Petén**: Parque Nacional Tikal, aguada del hotel Posada la Selva, 30 abr. 1970, *Ortíz 1049* (F, NY); ruinas Plaza Mayor Tikal, 333 m, 16 nov. 1965, *Molina 15281* (F, NY); 35 km E de Santa Elena, brecha El Remate-Tikal, 200 m, *Molina 15426* (F, NY, US); Tikal National Park, Tikal, growing around aguada at Camp, *Lundell 15918* (US). GUYANA. Within 30 mi. of Georgetown, *Rodway s.n.* (US). HAITÍ. Massif du Nord, *Ekman 4392* (US); Plaine de L'Artibonite, Dessalines, *Ekman 8534* (G). HONDURAS. **Atlántida**: La Fragua, 20 m, Feb. 1928, *Standley 55711* (F, US); Tela, near Lancetilla valley, 6 Dec. 1927, *Standley 53428* (F, US). **Francisco Morazán**: San Antonio de Oriente, 22 jul. 1945, *Rodríguez 3126* (F). MEXICO. **Campeche**: Tuxpeña, 18 Feb. 1932, *Lundell 1355* (F, GH, MO, NY, US); 70 km al E de Escárcega, 26 mar. 1982, *Cabrera & Cabrera 2237* (MEXU, MO). **Chiapas**: slopes and small streams with Tropical Rain Forest along the ridges 6–12 km south of Palenque on the road to Ocosingo, 300 m, 12 Oct. 1972, *Breedlove 28837* (MEXU, MO). **Colima**: Manzanillo, sea level, *Hitchcock 7031* (RB, US). **Oaxaca**: San Antonio, 2 Sep. 1894, *Pringle 5573** (F, GH, MEXU, MO, US); District of Tuxtepec, Chiltepec and vicinity, 200 m, *Martínez Calderón 568* (US). **Quintana Roo**: 4 km NW of J.M. Morelos, along Hwy. 184, at the place where it crosses the marshes of Laguna Chichancanab, 18 May 1982, *Davidse et al. 20612* (MEXU, MO); San José de la Montaña, 9 km S of Hwy. 186 on Hwy. to Tomás Garrido, 120 m, 9 May 1982, *Davidse et al. 20271* (MEXU, MO). **San Luis Potosí**: bank of Río Valles, 27 June 1910, *Leavenworth 199* (GH, MO). **Tabasco**: Boca Cerro, Tenosique, 1 jul. 1939, *Matuda 3577*** (F, GH, US); km 21 de la carretera Cárdenas–Coatzacoalcos, 17 sep. 1981, *Magaña 427* (MEXU, MO). **Veracruz**: Estación Biológica San Andrés Tuxtla, 27 nov. 1978, 150 m, *Martínez Calderón 1798* (F, MEXU, MO). **Yucatan**: Becanche, 19 ene. 1956, *Enriquez 347* (MEXU). NICARAGUA. **Zelaya**: vicinity of Waní, including Río Ulí, ca. 13°41′N, 84°50′W, 90–100 m, 22 Apr. 1978, *Stevens 7982* (MO). PANAMA. **Bocas del Toro**: 1 km NW of Bocatorito on SE side of island, 9 Feb. 1989, *Peterson & Annable 6729* (MO). **Colon**: 4 km E of Buena Vista, *Nee 6783* (MO). **Darién**: Darién, Sep. 1967, *Duke 14117* (F, MO, NY); Río Sabana, *Leopold 109* (MO). **Panama**: past Chepo and Río Mamoni on road to El Llano, 25 Sep. 1972, *Tyson 6791* (MO). **Zona del Canal**: Between Gorgona and Tabernilla, *Hitchcock 7964* (F, GH, K, MO, P, US). PERU. **Ucayali**: Canchahuayo, *Vásquez et al. 7025* (MO, SI). TRINIDAD Y TOBAGO. Little Tobago Island, 26 July 1914, *Broadway 4895* (US); 8 miles S of Mayaro, along Mayaro-Guayaguayare road, 1 Aug. 1970, *Davidse 2510* (MO); Parrott Hill, 22 July 1913, *Broadway 4586* (MO, NY, US). VENEZUELA. **Anzoategui**: Pariaguán, El Tigre, 16 jul. 1946, *Oropeza s.n.* (VEN). **Barinas**: Sistema de riego Río Boconó, *Trujillo 11399* (MY). **Delta Amacuro**: Isla Cocuina, en sitio intervenido, *Ramia 3330* (MY, VEN). **Falcon**: boca del Río Tocuyo, *Trujillo 11492* (MY); 7 km E of Mirimire, *Wingfield 5548* (MO). **Guárico**: Carretera Santa María de Ipire a El Socorro, 5 km antes del último poblado, 150 m, 17 ago. 1989, *Zuloaga et al. 4507** (MO, SI, VEN). **Miranda**: Río Grande del Tuy, above Paparo, *Pittier 6332* (US). **Portuguesa**: Dtto. Araure, en terrenos adyacentes a la vía que une Agua Blanca con Payara, *Rámirez Reyes 2051, 2054* (PORT). **Tachira**: Colonia Agropecuaria Los Andes, La Fría, 100 m, *Medina 1246* (VEN). **Trujillo**: La Mesa de Esmujaque, 1800 m, *Box 3703* (MY); cerca de Agua Viva, en las orillas del Río Motatán, *Tamayo 1768** (US, VEN). **Yaracuy**: Carretera entre Yaritagua y Barquimiseto, *Burandt Jr. V0238* (MO, VEN); San Felipe, orillas arenosas del Río Yaracuy, 11 abr. 1946, *Burkart 16447** (SI). **Zulia**: vicinity of Mene Grande, *Pittier 10620* (GH, US, VEN); San Martin, on Río del Palmar, *Pittier 10534* (GH, NY, US, VEN).

Esta especie es abundante en América Central y Colombia y Venezuela, siendo ocasional en el norte del Brasil. Sólo fue registrada una colección en Argentina, en las cercanías del límite con Paraguay.

Difiere del resto de especies de la sección por ser una planta de gran porte, con panojas amplias que llevan espiguillas pequeñas y por poseer vainas con pelos urticantes. Gould (1975), puntualiza que los pelos silíceos presentes en las vainas pueden causar irritación en la piel al contacto con los mismos.

18. Panicum hirticaule J. Presl, Reliq. Haenk. 1: 308. 1830. *Panicum polygamun* Sw. var. *hirticaule* (J. Presl) E. Fourn., Mexic. Pl. 2: 28. 1886. *Panicum capillare* L. var. *hirticaule* (J. Presl) Gould, Madroño 10: 94. 1949. TIPO: México. Guerrero: Acapulco, *Haenke s.n.*** (holótipo, PR no visto, fragmento, US-80698; isótipo, MO-1837663).

Plantas anuales, de 25–120(–150) cm de alto. *Cañas* decumbentes, arraigadas en los nudos inferiores a erectas, ramificadas hacia la base; entrenudos de 4–21 cm de largo, comprimidos, surcados, hirsutos; nudos cortamente hirsutos. *Vainas* de 3–10 cm de largo, más cortas que los entrenudos, hirsutas, con pelos tuberculados, verdosas a púrpuras, con un margen pestañoso, el restante glabro. *Lígulas* membranáceo-pestañosas, de 0.9–1.5 mm de largo; cuello hirsuto. *Láminas* lanceoladas a linear-lanceoladas, de 6–25(–31) cm de largo, 0.4–1.6(–2.2) cm de ancho, planas, hirsutas a esparcidamente pilosas, con pelos blanquecinos, tuberculados, de base subcordada, amplexicaule, el ápice subagudo, con los márgenes papiloso-pestañosos. *Pedúnculos* subincluidos en las vainas foliares a exertos, hasta de 36 cm de largo, híspidos a

glabros. *Inflorescencias* terminales, laxas, de 9–26(–30) cm de largo, 5–18 cm de ancho; *eje principal* anguloso, escabroso, glabro a esparcidamente piloso junto a la base; pulvínulos glabros; ramificaciones de primer orden alternas a subopuestas, en ocasiones subverticiladas, divergentes, glabras a esparcidamente pilosas hacia la base; ramificaciones de segundo orden adpresas con espiguillas adpresas; pedicelos de 0.9–2.7 mm de largo, escabriúsculos. *Inflorescencias axilares* presentes, similares a las terminales. *Espiguillas* ovoides, de 1.9–2.8(–3.5) mm de largo, 0.8–1 mm de ancho, abruptamente acuminadas, no estipitadas, glabras, cobrizas a violáceas; gluma superior y lemma inferior subiguales, superando hasta 0.8 mm en largo al antecio superior. *Gluma inferior* ovado-acuminada, de 1.3–2.4 mm de largo, ½–¾ del largo de la espiguilla, 3–5-nervia, nervio medio escabriúsculo a liso. *Gluma superior* de 1.8–2.9(–3.3) mm de largo, 7–9(–11)-nervia, con el nervio medio escabriúsculo hacia el ápice a liso. *Lemma inferior* glumiforme, de 1.8–2.8(–3.3) mm de largo, 9-nervia. *Pálea inferior* lanceolada a ovado-acuminada, de 0.4–0.9 mm de largo, 0.2–0.4 mm de ancho, ⅓–½ del largo del antecio superior, membranácea, hialina, glabra. *Antecio superior* elipsoide, de 1.5–2.3 mm de largo, 0.7–0.9 mm de ancho, crustáceo, glabro, liso, brillante a opaco, pajizo a negruzco, papiloso en toda la superficie, con papilas simples, o sólo presentes hacia el ápice de la pálea, con dos cicatrices basales ca. 0.2 mm de largo, castañas a la madurez; lemma 7-nervia. *Cariopsis* elipsoide, de 1–1.7 mm de largo, 0.7–0.8 mm de ancho, blanquecina; hilo punctiforme; embrión la mitad del largo de la cariopsis.

18a. **Panicum hirticaule** var. **hirticaule**

Panicum capillare L. var *miliaceum* Vasey, Contr. U.S. Natl. Herb. 1: 28. 1890, *non Panicum miliaceum* L., 1753. *Panicum sonorum* Beal, Grasses N. Amer. 2: 130. 1896. *Panicum hirticaule* J. Presl var. *miliaceum* (Vasey) Beetle, Phytologia 47: 381. 1981. TIPO: México. Sonora: Lerdo, 1889, *Palmer 947* (holótipo, US-2903025).

Panicum hirticaulon J. Presl var. *glabrescens* Andersson, Kongl. Vetensk. Acad. Handl. 1853: 135. 1855. TIPO: Ecuador. Archipiélago de Colón: Isla Chatham, *Andersson s.n.* (tipo no visto).

Espiguillas de 1.9–2.8(–3.3) mm de largo. *Antecio superior* pajizo, brillante, liso, con papilas simples hacia el ápice de la pálea.

Nombre vulgar. "Triguillo," "zacate de año," "zacate peludo perdis" (en México); "chiri-chiri" (en Perú).

Distribución y ecología. Abundante en el sur de Estados Unidos de América, México y Mesoamérica; menos frecuente en América del Sur donde crece en Ecuador, Perú y Venezuela (Fig. 11). Crece en ambientes abiertos, sobre suelos modificados, desde el nivel del mar hasta los 2500 m.

Material representativo citado. COSTA RICA. **Guanacaste:** Playas del Coco, S end of bay, 6 July 1968, *Pohl & Davidse 10653* (F, ISC, LA); upper slopes of bluffs above Pacific Ocean, S of Playas del Coco, 5 Aug. 1966, *Pohl & Calderón 10216* (ISC, MO). **Puntarenas**: vicinity of Cascajal, along road from Cascajal to Pigres, 30–100 m, 6 July 1949, *Holm & Iltis 286* (GH). ECUADOR. **Archipielago de Colon**: Isabela Island, Volcano Alcedo, *Fowler 8d* (MO); Indefatigable Island, 6 mi. north of Academy Bay, 10 Apr. 1930, *Svenson 236* (F, GH, LA). **Guayas**: Caperia, km 21, Guayaquil to Daule, 20–200 m, 15 Feb. 1982, *Dodson & Gentry 12506, 12514* (MO). EL SALVADOR. **La Libertad**: along road ca. 1 km NE of Hwy. CA-1, on road 9 km WSW of Quetzaltepeque, 18 June 1978, *Pohl & Gabel 13609** (F, ISC). **Santa Ana**: Lagunita Clara, 5 km S of Metapán, 500 m, 10 June 1970, *Pohl & Davidse 11872* (F, ISC, MO); along hwy. 12, 9 km N of Texistepeque, 550 m, 25 June 1978, *Pohl & Gabel 13665* (F, ISC, MO). **San Salvador**: Apulo, in pasture slopes near Lake Ilopango, 18 June 1949, *Williams & Molina 16751* (F). **Sin Provincia**: San Andrés, 1700 ft. 1943, *Walkins 17* (US); La Cabaña, 300 m, 12 July 1943, *Walkins s.n.* (US-2437900); west side of Lake Ilopango, 23 Nov. 1911, *Hitchcock 8924* (US). ESTADOS UNIDOS DE AMERICA. **Arizona**: Pima Co., near base of trail to top of Mt. Baboquivari, 14 Sep. 1947, *Gould 4468* (LA, MO); Gila County, Pocket Creek Canyon, Sierra Ancha Mountains, 29 Aug. 1946, *Gould & Hudson 3748* (GH, LA). **New Mexico:** Cedar Spring, *Mulford 1078* (MO); 1 mi. W of Hillsboro, 6000 ft., 2 Oct. 1904, *Metcalfe 1442* (GH, LA, US). **Texas:** 1 mi. SE of College Station, 21 Apr. 1940, *Evans s.n.* (US-2434928); El Paso, 10 Sep. 1884, *Jones s.n.* (LA-39220). **Washington**: W. Klickitat Co., bottom land near Bingen, Nov. 1894, *Suksdorf 2330* (GH, LA, MO). GUATEMALA. **Izabal**: Los Amantes, 9 mayo 1919, *Blake 7326A* (US); vicinity of Puertos Barrios, 2 July 1922, *Standley s.n.* (US). **Suchitepequez**: South of Alotenango Farm, 7 miles south of Tiquisate along road within 3 miles of ocean, 19 June 1942, *Steyermark 47766* (F); Tiquisate, 100 m, 19 June 1942, *Steyermark 47859* (F, US). **Zacapa**: rocky slopes between San Pablo and Pepezca, 200–250 m, 8 Oct. 1939, *Steyermark 29326* (F); vicinity of Zacapa, 200 m, 6 Oct. 1940, *Standley 74383* (F). **Sin Estado**: near ruins of Quiriguá, 28 Feb. 1932, *Weatherwax 79a* (US); between San Andrés and Muluá, 12 Apr. 1932, *Weatherwax 217* (US). HAITÍ: Plaine Cul-de-Sac, Port-au-Price, Damine, in fields, 25 mayo 1928, *Ekman 9991* (G, US). HONDURAS. **Choluteca**: 7 km by road NE of Choluteca, 50 m, 4 July 1970, *Pohl & Davidse 12177*** (F, ISC, MO). **Comayagua**: Comayagua, Estación Agrícola El Carao, 630 m, 30 jul. 1983, *Casco 46* (MO). **Cortés**: San Pedro Sula, Hacienda Monte Moria, 16 abr. 1984, *Cristoff 181* (NY). **Francisco Morazán**: Tegucigalpa, cerro El Berrinche, 1000 m, 6 ago. 1978, *Castro 69* (MEXU, MO). **Valle**: 4 km SE of San Lorenzo, 0–5 m, 5 Oct. 1986, *Davidse & Pilz 31665** (MO). MEXICO. **Baja California Sur**: km 65 east of San Antonio, 6 June 1973, *Beetle M-2551* (MO); Mesa de San Gerónimo, northerly from Rancho Viejo (on road from Loreto to San Javier), 23 Sep. 1965, *Carter 5016* (LA, MEXU).

Chiapas: marshes along Rio Usumacinta, 25–30 km east northeast of Palenque Junction, 30 m, 12 Dec. 1981, *Breedlove 56081* (MO, NY); forest at Mirador for Chicoasen Dam along road from Tuxtla Gutiérrez to the Chicoasen Dam, 850 m, 17 Nov. 1976, *Breedlove 41540* (MO). **Chihuahua**: N end of E side of Sierra del Cuchillo Parado, 29°37′N, 104°55′W, 1000–1300 m, 21 Oct. 1972, *Wendt et al. 9788* (MO, NY); 20 Km S of Ciudad Camargo, 1220 m, 1 July 1939, *Harvey 1378* (GH, MO, US); Guasaremos, Río Mayo, 20 Sep. 1935, *Gentry 1841* (MEXU, MO, US). **Chihuahua-Sonora**: Rancho Carreteras, 1460 m, 26 ago. 1939, *Harvey 1600* (MO, US). **Colima**: Alzada, 21 Sep. 1910, *Hitchcock 7089** (US); Colima, July 1897, *Palmer 143* (ISC, NY, US, W). **Durango**: 10 km N of Ceballos and 8½ S of Chihuahua state line on the Torreon-Chihuahua highway, 1200 m, 26°36′N, 102°12′W, *Johnston et al. 12292* (MO). **Guerrero**: south Chilpacingo, 7 Dec. 1941, *Leavenworth 966* (MO); Río Balsas, 26 ago. 1910, *Orcutt 4197* (MO). **Guanajuato**: Irapuato, 5800 ft., 1 Oct. 1910, *Hitchcock 7424* (US). **Jalisco**: ca. 5 road-miles SW of Santa Cruz de las Flores, 1550 m, 24 Aug. 1957, *McVaugh 16326* (MEXU, NY, US); Tecalitlán, al S de Tecalitlán, rumbo a Pihuamo, 12 Aug. 1987, *Ornelas U. et al. 1167* (MEXU). **Mexico**: Temascaltepec, Anonas, 24 July 1934, *Hinton 6337* (MO, NY, US); Temascaltepec, Barranca, Ixtapán, 1000 m, *Hinton 1062* (F, MEXU, NY, US). **Michoacán**: Chavinda, 27 Sep. 1946, *Hernández Xolocotzi et al. x-2775* (US); at edge of tropical deciduous forest, La Majada, 8 May 1941, *Leavenworth & Hoogstrall 1335* (GH, NY). **Nayarit**: 1 mile west of Mazatán, 600 m, 17 Sep. 1960, *McVaugh 19117* (NY, US); near km 31, 4–5 miles N of Compostela, 22 Sep. 1960, *McVaugh 19333* (NY, US). **Oaxaca**: 2 km al SE de San Martín Toxpalán, por carretera a Teotitlán del Camino, 26 ago. 1980, *Medrano et al. F-1495* (MO); Los Tules Niltepec, 11 dic. 1985, *Torres C. et al. 7860* (MEXU, MO). **Sonora**: El Rancho de la Nacha, 25 mi. W of La Angostura, 4300 ft., 14–20 Aug. 1941, *Vera Santos 1850* (GH, LA, MO, NY); 27 miles west of Hermosillo on the road to Kino Bay, 720 ft., 28 Aug. 1941, *Wiggins & Rollins 137* (GH, LA, MO, NY). **Tabasco**: km 6.6 de Emiliano Zapata hacia Tenosique, 5 jul. 1981, *Cowan 3398* (MEXU, MO). **Veracruz**: La Mancha, carretera Cardel-Nautla, 1 ago. 1971, *Dorantes 246bis* (F, GH); Baños del Carrizal, *Purpus 6212* (GH, LA, MO, NY). **Yucatán**: Chichankarrab, *Gaumer 1501* (F). NICARAGUA. **Estelí**: Kukamonga km 167, Portal de Belén, 1 ago. 1983, *Moreno 21833* (ISC, MO); faldas del Chayo 13°16′N, 86°20′W, 700–1000 m, 31 jul. 1983, *Moreno 21790* (ISC, MO). **León**: along Hwy. 12, 4 km S of road to Puerto Somoza, 50 m, 18 July 1970, *Pohl & Davidse 12369* (F, MO). **Managua**: km 24 on Hwy. 12 (Carretera vieja a León), 7 km WSW of summit of Sierra de Managua, ca. 12°04′N, 86°26′W, ca. 200 m, 7 July 1977, *Stevens 2672* (F, ISC, MO); Rte. 1, 12 km E of Managua, 1 Aug. 1972, *Seymour 6275* (MO). **Masaya**: km 17.5 carretera Managua-Masaya, terrenos de la UCA, 12°01′N, 86°10′W, 10 jun. 1982, *Sandino* 3038 (MO). **Rivas**: Isla Ometepe, Volcán Maderas, cafetal Las Cuchillas, 11°28′–29′N, 85°29–30′W, 200–300 m, 23 sep. 1984, *Robleto 1269* (ISC, MO, SI); along CIA, near Lago de Nicaragua, 24 km SE of Rivas, 1 Aug. 1971, *Pohl 12674* (F, ISC, MO). PANAMÁ. **Panamá**: Taboga Island, Dec. 1923, *Standley 27960* (US). **Zona del Canal**: Chiva Chiva trail near Miraflores Lake, 30 Sep. 1965, *Tyson 1396* (MO); Balboa, Sosa Hill, Dec. 1923, *Standley 25277* (MO, US). PERU. **Cajamarca**: Prov. Cajamarca, alrededores de Choropampa, sobre la carretera de penetración Pacasmayo-Cajamarca, a la altura del km 124, anual, en bordes de campos de cultivo y laderas no cultivadas, 7 mar. 1981, *Sánchez Vega 2363** (MO, SI, US). **Huánuco**: Huánuco, in cornfield, loose clumps, subdecumbent below, 28 Apr. 1923, *McBride 3526* (F, US). **La Libertad**: Prov. Trujillo, Chual-Cruz de Cascaday, 1200 m, 29 mar. 1953, *Lopez Miranda 951* (US). **Piura**: Prov. Talara, alrededores de Talara, 15 oct. 1983, *Sagástegui 10912* (MO, SI); 40 km west of Piura, 50 m, 29 Mar. 1939, *Stork & Horton 11361* (F, MO). VENEZUELA. **Guárico**: El Socorro, 15 July 1946, *Burkart 17204* (SI); Carretera Santa María de Ipire a El Socorro, 08°58′N, 65°40′W, 150 m, 17 ago. 1989, *Zuloaga et al. 4508** (MO, SI, VEN).

Especie afín a *P. stramineum* y *P. ghiesbreghtii*. De *P. stramineum* se distingue por poseer pálea inferior reducida, espiguillas cobrizas a violáceas, dispuestas densamente en las ramificaciones, siendo estas adpresas. *Panicum ghiesbreghtii* se distingue por ser una especie perenne, con láminas más angostas y de mayor tamaño, de 16–30(–55) cm de largo.

El tamaño de las espiguillas en *P. hirticaule* normalmente varía entre 1.9 y 2.8 mm de longitud. Se observaron algunos ejemplares de México y Estados Unidos con espiguillas hasta de 3.5 mm de longitud, los que poseen asimismo la base del antecio superior redondeada. Existen también varios especímenes del Perú, de los departamentos Huánuco, La Libertad y Loja (*Sánchez Vega 2338, 2363, Cabanillas et al. 15, 17, Ochoa 1584, McBride 3526, López Miranda 951* y *Ridoult 1919*), de mayor porte y con espiguillas de aproximadamente 3.3–3.5 mm de largo.

Hitchcock (1927) cita *P. hirticaule* para el Perú sobre la base de dos ejemplares: *Hitchcock 22115* y *McBride 2536*. El primero de estos corresponde a *P. exiguum* y el segundo a *P. hirticaule* con espiguillas mayores. Swallen (1943) cita esta especie para Bolivia, sin mencionar ejemplar de herbario; probablemente esta cita corresponde a *P. stramineum*.

Swallen (1964) y Tovar (1993) citan la presencia de *P. hirticaule* en Argentina sin mencionar ejemplares de referencia.

18b. Panicum hirticaule var. **verrucosum** Zuloaga & Morrone, var. nov. TIPO: México. Chihuahua: between Casas Grandes and Sabinal, 4 Sep. 1989, *Nelson 6355* (holótipo, US; isótipo, GH).

Panico hirticauli affine sed anthoecio papillato, papillis verrucosis omnino paginae differt.

Espiguillas de 2.4–3.5 mm de largo. *Antecio superior* negruzco, opaco, con conspicuas papilas simples en toda su superficie (Fig. 1A, B).

Distribución y ecología. Sur de los Estados

Unidos, en Arizona, y norte de México, en los estados de Chihuahua, Guerrero, Jalisco, Nayarit, Sinaloa y Sonora (Fig. 3). Se halla en campos; llega hasta los 600 m.

Nombre vulgar. "Zacahuastle" (en México).

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **Arizona**: near Fresnal, Papago Indian Reservation, 30 Sep. 1934, *Peebles 10366* (GH, US); Pima County, South Canyon, Baboquivani Mts., 15 Sep. 1931, *Gilman 37* (GH); Tucson Mountains, 25 Aug. 1904, *Griffiths 6939 1/2, pr. p.* (US); 7 miles N of Nogales, US highway 89, Ruby Road to Peña Blanca Recreation Park, 1 Aug. 1959, *Soderstrom 160* (US); north slope of Santa Rita Mountains, 13/21 Sep. 1904, *Griffiths 7194* (US). MEXICO. **Chihuahua**: Chapingo, *Hernández & Tapia 240** (US). **Guerrero**: Cuautepec, San Agustín Cuilutia, 10 jul. 1986, *Herrera Castro 84* (MEXU). **Jalisco**: Amatitán, Barranca Santa Rosa, orilla del Río Santiago, 600 m, 4 ago. 1977, *Villarreal 6661** (MEXU). **Nayarit**: El Nayar, Jesús María, 600 m 4 ago. 1977, *Colunga & Zizumbo 44*** (MEXU). **Sinaloa**: alrededores del dique La Primavera, selva baja caducifolia a 10 km al sur de Culiacán, 60 m, *Aviña 1248* (MEXU). **Sonora**: sin localidad, 17 sep. 1908, *Hitchcock 3526* (US), *Wiggins 6023* (US).

En el ejemplar *Gilman 37* las papilas son diminutas, el antecio superior es brilloso y la gluma superior se cae en algunas espiguillas.

Una porción del ejemplar *Griffiths 6939 1/2* corresponde a esta variedad (las otras dos plantas de esta colección son *P. pampinosum*). Hitchcock & Chase (1910) y Fairbrothers (1953) lo citan dentro de *P. hirticaule.*

En el ejemplar *Peebles 10366* las espiguillas llegan excepcionalmente a tener 3.8 mm de largo.

19. Panicum hispidifolium Swallen, Contr. U.S. Natl. Herb. 29: 424. 1950. *Panicum hispidum* Swallen, Contr. U.S. Natl. Herb. 29: 269. 1949, non G. Forst., 1786. TIPO: Honduras. El Paraíso: Güinope, 1430 m, 1 ene. 1944, *Rodríguez 1981*** (holótipo, US-1869144; isótipos, F-1166244, 1306220). Figura 22.

Panicum flabellatum E. Fournier, Bull. Soc. Bot. France, ser. 2, 27: 293. 1880, non Steud., 1853. TIPO: Nicaragua. Managua: Isla de Omotepe, oct. 1869, *Levy 1166* (holótipo, P, fragmento, US-80615; isótipos, G, P).

Plantas anuales, herbáceas. *Cañas* cespitosas, erguidas, simples, de 20–100 cm de alto, geniculadas o no en los nudos inferiores; entrenudos cilíndricos, huecos, de 4–15 cm de largo, 0.1–0.4 cm diám., hirsutos, con pelos tuberculados caedizos; nudos pilosos, violáceos. *Vainas* de 4–13 cm de largo, menores o mayores que los entrenudos, densamente hirsutas, con largos pelos tuberculados, los márgenes pestañosos. *Lígulas* cortamente membranáceas en la base, luego largamente ciliadas, de 2–3 mm de largo; cuello piloso, violáceo. *Láminas* linear-lanceoladas, de 8–45 cm de largo, 0.8–1.3 cm de ancho, planas, herbáceas, acuminadas, subcordadas o de base redondeada, hirsutas, con bordes escabrosos, ciliados hacia la base, el nervio medio manifiesto. *Pedúnculos* incluidos en las vainas foliares a exertos, hasta de 40 cm de largo, cilíndricos, hirsutos. *Inflorescencias* terminales exertas; panojas laxas, difusas, piramidales, multifloras, de 12–50 cm de largo, 10–40 cm de ancho; *eje principal* anguloso, híspido, cubierto de gruesos pelos de base tuberculada, glabro hacia la porción superior de las panojas; pulvínulos pilosos; ramificaciones opuestas o alternas, las inferiores ocasionalmente subverticiladas, divergentes, hasta de 17 cm de largo; ejes de las ramificaciones híspidos, con espiguillas distantes, no adpresas; pedicelos largos, de 0.5–2.5 mm de largo, escabrosos. *Inflorescencias axilares* presentes, semejantes a las terminales. *Espiguillas* globosas, abiertas en el ápice, de 3.2–3.7 mm de largo, 1.2–1.6 mm de ancho, solitarias, no estipitadas, glabras, verdosas y con tintes violáceos, agudas a acuminadas, glumas y lemma inferior con nervios marcados; gluma superior y lemma inferior subiguales o superando hasta 0.3 mm en largo al antecio superior. *Gluma inferior* ovada, de 2–2.6 mm de largo, ½–¾ del largo de la espiguilla, aguda, 5-nervia, el nervio medio escabroso, escabriúscula hacia el ápice de la cara interna. *Gluma superior* de aproximadamente igual largo que la espiguilla, aguda, 7-nervia, el nervio medio escabriúsculo hacia el ápice, escabriúscula en el ápice de la cara interna; gluma inferior y superior separadas por un corto entrenudo ca. 0.3 mm de largo. *Lemma inferior* glumiforme, 7–9-nervia, aguda, pilosa en el ápice de la cara interna. *Pálea inferior* ovado-lanceolada, reducida, de 1.6–1.8 mm de largo, 0.6–0.9 mm de ancho, ¾ del largo del antecio superior, hialina, los bordes superiores esparcidamente pilosos a glabros, glabra en el resto de la superficie. *Antecio superior* anchamente ovoide, de 2.1–2.5 mm de largo, 1.2–1.5 mm de ancho, crustáceo, glabro, liso, lustroso, con tintes grisáceos a la madurez y un anillo en la base, castaño a la madurez; lemma 7-nervia; pálea con papilas verrugosas hacia el ápice. *Cariopsis* anchamente ovoide, de 1.6–1.8 mm de largo, 1.1–1.3 mm de ancho; hilo punctiforme; embrión menos de la mitad del largo de la cariopsis.

Distribución y ecología. Se halla desde México y América Central, en El Salvador, Honduras, Nicaragua, Costa Rica, hasta Colombia y Venezuela (Fig. 8). Crece en sabanas; es frecuente en borde

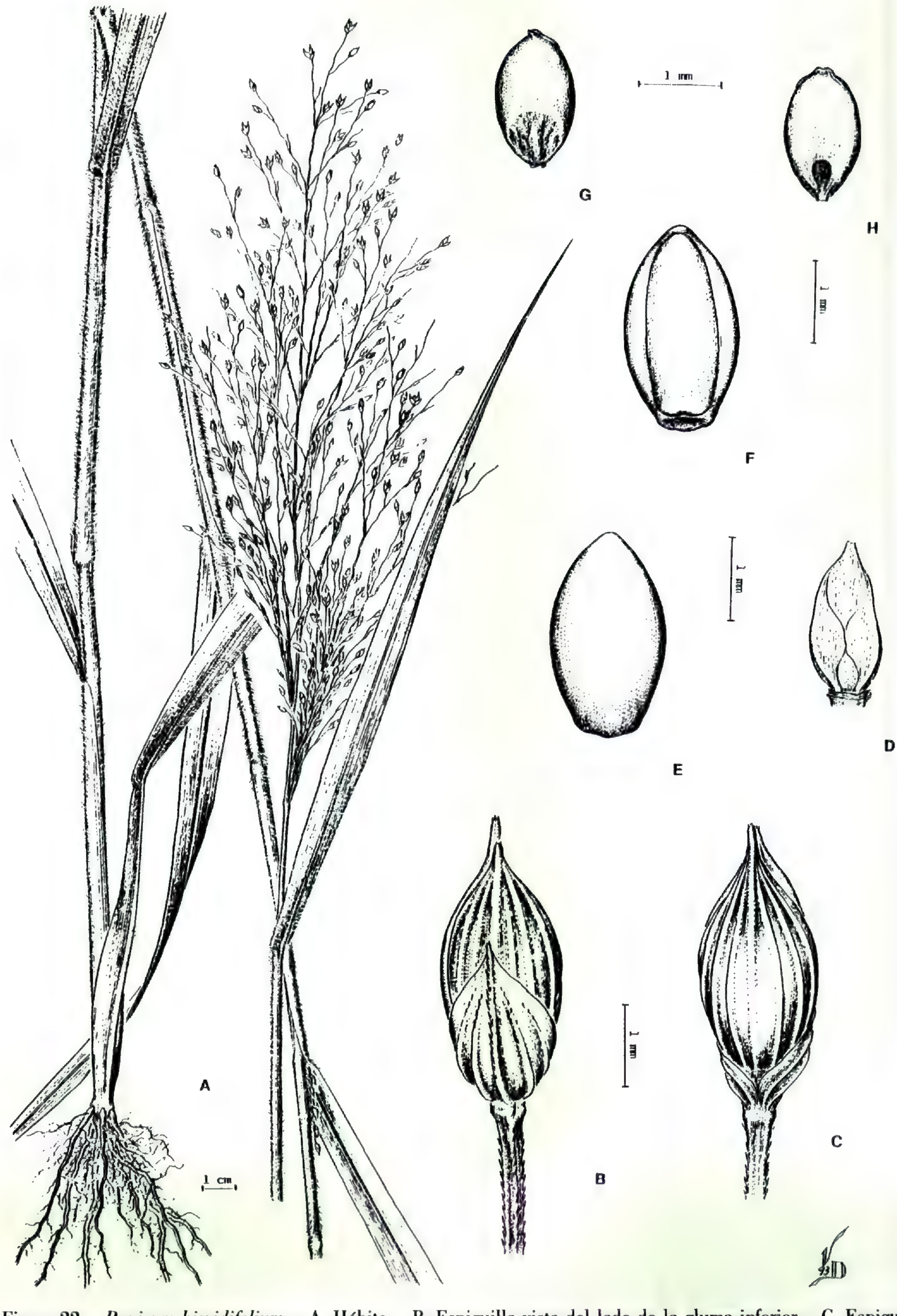


Figura 22. *Panicum hispidifolium.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Pálea inferior.—E. Antecio superior visto del lado de la lemma.—F. Antecio superior visto del lado de la pálea.—G. Cariopsis, vista escutelar.—H. Cariopsis, vista hilar. (*Zuloaga et al. 4363.*)

de caminos. Habita entre los 60 y 1430 m; florece y fructifica entre julio y diciembre.

Material representativo citado. COLOMBIA. **Atlantico**: Puerto de Colombia, *Hitchcock 9927* (US). **Magdalena**: Santa Marta, *Smith 2152* (F, G, GH, K, MO, NY, P, US). COSTA RICA. **Guanacaste**: 7 km N of Bagaces along the Carretera Interamericana, 100 m, 23 Oct. 1968, *Pohl & Davidse 11291* (F, MEXU); 5 km S of La Cruz, 200 m, *Pohl & Gabel 13703* (F, MO); 5 km SE of Liberia, on the Cañas road, 1966, *Harris 40** (F). EL SALVADOR. **Morazán**: 2 km W of Las Delicias, 13 Sep. 1951, 650 m, *Rohweder 2507* (MO). HONDURAS. **Cortes**: Ocote Arrancado, 50 km N Lago de Yajoa, 600 m, bosque tropical húmedo, nov. 1980, *Nelson et al. 5621* (MO). **El Paraíso**: Road to Yuscarán, moist places around rocks, about km 2, *Swallen 11344* (US). **Francisco Morazán**: road between El Jicarito and El Pedregal, 800–950 m, 13 Nov. 1948, *Standley 14492* (F); vicinity of El Zamorano, *Swallen 11264* (F, MO, US); vicinity of Las Mesas, ca. 5 km E of Zamorano, 3 Oct. 1986, *Davidse & Pilz 31533** (MO, SI). MEXICO. **Chiapas**: 58 km south of Mexican Highway 190 on road to Nueva Concordia, 900 m, 11 Sep. 1974, *Breedlove 37573, 37654* (MEXU, MO). **Oaxaca**: near road nine miles toward Tehuantepec from Zanatepec, *Morley 696* (F, GH, LA, MO). NICARAGUA. **Masaya**: Piedra Quemada, 1 km NW of Volcán Santiago, 350 m, 28 Oct. 1976, *Neill 1115* (MO). VENEZUELA. **Anzoátegui**: a 33 km al oeste de El Tigre, carretera a Pariaguán, 8°56′N, 64°35′W, 250 m, 17 ago. 1989, *Zuloaga et al. 4504** (MO, SI, VEN). **Apure**: Bajo Apure, *Ramia & Montes 4831* (VEN). **Aragua**: Rancho Grande, Parque Nacional Henry Pittier, 480 m, sabanas de loma pedregosa, *Montaldo & Ramia 3304* (MY). **Bolívar**: road to Salto Chavaripo, 88.7 km SW of Caicara del Orinoco, 7°7′N, 66°28′W, *Steyermark et al. 131327* (MO). **Cojedes**: Galeras del Pao, ago. 1980, *Ramia 7201*, (VEN); San Carlos, Sabanas entre San Carlos y Manrique, 29 sep. 1978, *Garófalo 163** (VEN). **Guárico**: carretera Calabozo–El Sombrero, a 7 km antes de la última población, 9°03′N, 67°3′W, 250 m, *Zuloaga et al. 4363** (MO, SI, VEN); 12 km de Calabozo, *Davidse 2950* (MO, VEN); entre El Sombrero y Pitara Bridge, *Pittier 12511* (NY, US, VEN). **Monagas**: sin localidad, *Larez 605* (VEN). **Portuguesa**: Dtto. Ospino, alrededores de carretera y comienzos de primera bajada hacia Ospino, *Rámirez Reyes 1773* (MO, PORT); Dtto. Guanare, orilla de carretera entre Las Matas y San Rafael, *Rámirez Reyes 1715* (PORT). **Trujillo**: vicinity of Dividive, *Pittier 10830* (GH, NY, US, VEN); Llanos de Trujillo, *Muller 987* (VEN).

Especie afín a *P. hirticaule*, de la que se diferencia por poseer espiguillas globosas de mayor tamaño, no adpresas y distantes, por tener inflorescencias difusas que alcanzan aproximadamente ½ del largo total de la planta y lígulas de 2–3 mm de largo.

Swallen (1955) considera erróneamente en la sinonimia de *P. hirticaule* a *P. flabellatum*, cuyo tipo coincide con *P. hispidifolium*.

20. Panicum lepidulum Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 75, fig. 64. 1910. TIPO: México. Chihuahua: rocky hills near Chihuahua, 22 Sep. 1885, *Pringle 497*,*** (holótipo, US 155163; isótipos, F, MEXU, NY, US-742174, W). Figura 23.

Plantas perennes, cespitosas, con rizomas de entrenudos cortos. *Cañas* erectas, paucinodes, de (15–)25–70 cm de alto, simples, con innovaciones intravaginales naciendo en los nudos inferiores; entrenudos de 4–17 cm de largo, cilíndricos, hirsutos a glabros, de 1–2 mm de diámetro; nudos pilosos. *Vainas* por lo general más cortas que los entrenudos, hirsutas con pelos tuberculados, usualmente con tíntes purpúreos, los márgenes pestañosos. *Lígulas* membranáceo-pestañosas, de (1–)2(–3) mm de largo; cuello piloso. *Láminas* linear-lanceoladas, de 8–26 cm de largo, 0.4–1.2 cm de ancho, erectas, ascendentes, más o menos adpresas al eje, planas o con los bordes involutos, hirsutas, con pelos tuberculados, ocasionalmente glabras, de base redondeada y ápice acuminado, los márgenes escabriúsculos, pestañosos hacia la base, el nervio medio manifiesto. *Pedúnculos* hasta de 30 cm de largo, glabros a hirsutos. *Inflorescencias* terminales exertas, laxas, difusas, de 7–20 cm de largo, 4–10 cm de ancho; *eje principal* hirsuto hacia la porción basal a glabro, escabroso en el resto de la superficie; pulvínulos glabros; ramificaciones de primer orden ascendentes; ramas de segundo orden divergentes, llevando 1–3 espiguillas solitarias; pedicelos de 2–12 mm de largo. *Espiguillas* largamente ovoides, de (3.3–)3.6–4.2 mm de largo, 1.2–1.5 mm de ancho, agudas, no estipitadas, glabras, verdosas o con tintes purpúreos; gluma superior y lemma inferior subiguales, 0.9–1.5 mm más largas que el antecio superior. *Gluma inferior* ovada, de 1.6–1.9 mm de largo, ½ o algo menor del largo de la espiguilla, aguda, 5-nervia, el nervio medio escabriúsculo hacia el ápice. *Gluma superior* acuminada, de 3.3–3.6 mm de largo, 9–15-nervia, el nervio medio escabriúsculo hacia el ápice. *Lemma inferior* acuminada, de 3.3–3.9 mm de largo, 9-nervia, el nervio medio escabriúsculo hacia el ápice. *Pálea inferior* reducida, ovada, de 1.5–2 mm de largo, 0.7–0.9 mm de ancho, ¾ del largo del antecio superior, hialina, glabra. *Antecio superior* ovoide, de 2.1–2.5 mm de largo, 1–1.5 mm de ancho, crustáceo, glabro, liso, lustroso, pajizo, con un anillo circular en la base, castaño a la madurez; lemma 7-nervia; pálea con papilas simples y micropelos globosos hacia el ápice. *Cariopsis* ovoide, de 1.8 mm de largo, 1 mm de ancho; hilo oblongo; embrión ½ del largo de la cariopsis.

Distribución y ecología. Abundante en México y ocasional en Guatemala (Fig. 8), crece en sabanas o en bosques de robles, sobre suelos a menudos volcánicos; se halla también en bordes de caminos. Llega hasta los 2400 m; florece entre marzo y octubre.

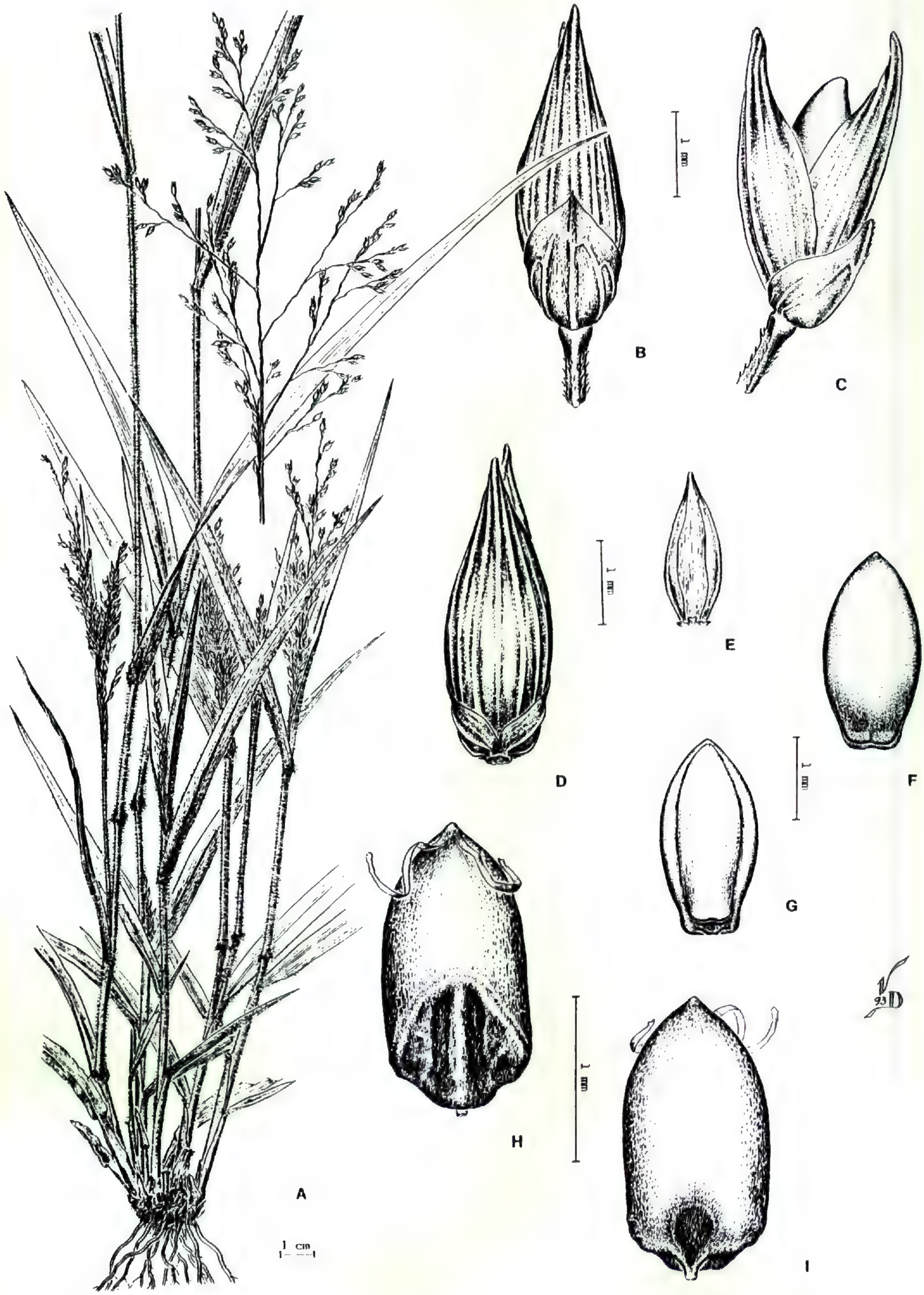


Figura 23. *Panicum lepidulum.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla, vista lateral.—D. Espiguilla vista del lado de la gluma superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Cariopsis, vista escutelar.—I. Cariopsis, vista hilar. (A–G, *Davidse & Davidse 9927*; H, I, *Arsène 2864.*)

Material representativo citado. GUATEMALA. Guatemala city, *Hitchcock 9014* (US). MEXICO. **Aguascalientes**: 8 mi. E of Calvillo, 6900 ft., 25 Sep. 1963, *Reeder & Reeder 3814* (US). **Chiapas**: Arriaga, savanna 2 km SE of Arriaga, *Breedlove 36852* (NY). **Chihuahua**: 12.8 mi. W of General Trias on Rte. 16, ca. 1780, 21 Aug. 1979, *Wagner & Solomon 4341** (MO). **Coahuila**: Sierra de la Madera, vicinity of La Cueva, *Johnston 9104** (GH). **Distrito Federal**: near Mexico city, Pedregal, *Hitchcock 5958* (F, GH, NY, US). **Durango**: Durango, *Palmer 525** (F, GH, MEXU, MO, NY, RB, US); 46 miles NE of Durango on the Durango–Torreón road, 6300 ft., 30 Sep. 1959, *Soderstrom 812* (MEXU, US). **Guanajuato**: about 3 km NE of San Miguel, occasional in rocky soil near the top of Cerro de La Presa, *Sohns 504* (US); Santa Cruz de Juventino Rosas rumbo a Guanajuato, 2 sep. 1981, *Beetle M-7324* (MO). **Hidalgo**: steep rocky volcanic outcrops at head of descent into Barranca de Metztitlán between Zoquital and Los Venados, 2000 m, *Moore Jr. 4218* (GH, US). **Jalisco**: Paso de la Troje, near km 36, southwest of Ojuelos on road to Aguascalientes, rocky slopes on and near Cerro La Campana, *McVaugh 16819* (NY, US); ca. 7 mi. SE of the junction of Hwy. 80 and 45 at Lagos de Moreno, 1800 m, 21 Aug. 1975, *Davidse & Davidse 9927** (MO). **Mexico**: 3 km al W de San Cristóbal Ecatepec, base de la Sierra de Guadalupe, 2400 m, 18 ago. 1974, *Rzedowski 32145* (MEXU). **Michoacán**: ca. 16 miles N of the junction of highways 37 and 15, *Davidse 9912** (MO); vicinity of Morelia, *Arsène 2417** (GH, MEXU, MO, NY, US). **Morelos**: Barranca de Atzingo, 1900-2000 m, 7 mar. 1972, *Vázquez 3592* (MEXU). **Oaxaca**: Hacienda Aguilar, 1580 m, 23 jul. 1919, *Conzatti 3603* (US); 13.5 mi. SW of Sola de Vega along the road to Puerto Escondido, 1920 m, 14 Aug. 1975, *Davidse 9657* (MO). **Puebla**: Tehuacán, 5500 ft., *Hitchcock 6063* (MEXU, US). **Querétaro**: Near San Juan del Río, 18 Aug. 1905, *Rose et al. 9555* (MEXU, NY, US). **San Luis Potosí**: Las Canoas, 20 July 1910, *Hitchcock 5756* (US); 8 km al W de San Lorenzo, km 62 carretera S.L. Potosí-A. Morelos, 1800 m, *Rzedowski 565* (US). **Sonora**: Valle de Teras, near La Angostura, *White 3542** (GH). **Zacatecas**: Chapingo, km 846 carretera Juárez, 26 km al N de Fresnillo cerca de Tropico de Cáncer, 2150 m, 12 sep. 1955, *Hernández & Mathus n-1667* (US).

Panicum lepidulum es afin a *P. pampinosum* y *P. parcum*. *Panicum pampinosum* se distingue por incluir plantas anuales, con inflorescencias con las ramificaciones poco divergentes del eje, y por tener las espiguillas con la gluma inferior $^4/_5$ del largo de la espiguilla. *Panicum parcum* se caracteriza por incluir plantas anuales, con espiguillas estipitadas y gluma inferior ¾ del largo de la espiguilla.

Hitchcock (1951) cita esta especie para Utah, New Mexico y Arizona y Waller (1976) para Arizona, sin citar especímenes de herbario. No fue posible hallar ejemplares de *P. lepidulum* para los Estados Unidos en los herbarios examinados de ese país, por lo que dichas citas se consideran dudosas.

21. Panicum magnispicula Zuloaga, Morrone & Valls, Iheringia, Bot., 42: 5, figs. 9–17, 26 y 27. 1992. TIPO: Brasil. Santa Catarina: Água Doce, campo graminoso em encosta íngreme com afloramentos, 7.2 km ao sul da divisa Paraná-Santa Catarina ao longo da rodovia BR-153, 1160 m, 3 dic. 1987, *Valls, Gomes & Silva 11521** (holótipo, CEN; isótipo, SI). Figura 24.

Plantas perennes, cespitosas. *Cañas* floríferas erectas de 20–30 cm de alto, simples; entrenudos cilíndricos, huecos, glabros; nudos glabros. *Vainas* estriadas, más largas que los entrenudos, hirsutas, con pelos tuberculados blanquecinos, los bordes superiores largamente pestanosos. *Lígulas* membranáceo-ciliadas, reducidas, ca. 0.5 mm de largo. *Láminas* linear-lanceoladas, de 10–12 cm de largo, 0.2 cm de ancho, de base redondeada y ápice largamente atenuado, hirsutas, con largos pelos tuberculados a híspidas, los bordes ciliados, involutos. *Pedúnculos* ca. 25 cm de largo, cilíndricos, glabros. *Inflorescencias* terminales exertas; espiciformes a subespiciformes, paucifloras, de 3–6 cm de largo, 1 cm de ancho, con aproximadamente 7–12 espiguillas por panoja; *eje principal* y eje de las ramificaciones angulosos, escabrosos; pulvínulos pilosos; ramificaciones por panoja 3–4, las inferiores de 3 cm de largo; espiguillas solitarias y adpresas sobre los ejes; pedicelos claviformes, escabrosos y con largos pelos cerca de la inserción de la espiguilla. *Espiguillas* largamente elipsoides, de 5.5–5.8 mm de largo, 1.8–2 mm de ancho, estipitadas, glabras, verdosas o con tintes violáceos, con gluma superior y lemma inferior subiguales y superando en largo al antecio superior, de ápice atenuado. *Gluma inferior* de 3.5 mm de largo, ¾ o más del largo de la espiguilla, aguda, 7–9-nervia, el nervio medio escabriúsculo hacia la porción superior, separada de la gluma superior por un entrenudo conspicuo de 0.5 mm de largo. *Gluma superior* acuminada, 9-nervia, cortamente pilosa hacia el ápice en la cara interna. *Lemma inferior* acuminada, 9-nervia, violácea hacia la porción superior. *Pálea inferior* elíptica a lanceolada, reducida, de 2.5–2.8 mm de largo, 1–1.2 mm de ancho, ¾ del largo del antecio superior, hialina, glabra, ciliolada en los márgenes a glabra. *Antecio superior* largamente elipsoide, de 3.4–3.6 mm de largo, 1.5–1.7 mm de ancho, glabro, crustáceo, pajizo, lustroso, papiloso, con papilas distribuidas regularmente en toda la superficie de la pálea superior y en menor número sobre la lemma, con un anillo castaño circular en la zona de inserción con la raquilla; lemma 7-nervia; pálea con papilas simples en toda su superficie.

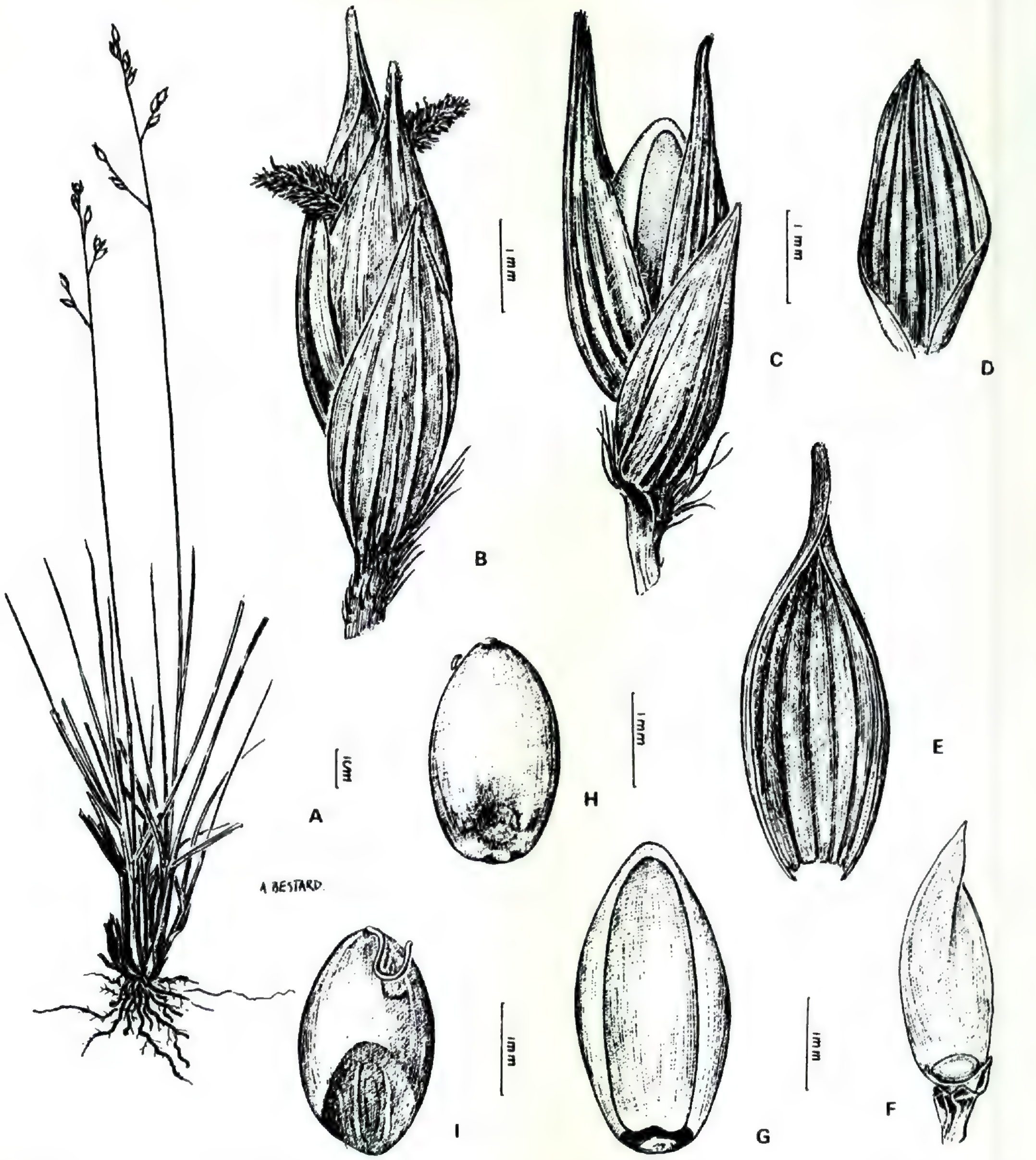


Figura 24. *Panicum magnispicula.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla, vista lateral.—D. Gluma inferior.—E. Gluma superior.—F. Pálea inferior.—G. Antecio superior vista del lado de la pálea.—H. Cariopsis, vista hilar.—I. Cariopsis, vista escutelar. (*Valls et al. 11521.*)

Cariopsis elipsoide de 2.2 mm de largo, 1.3 mm de ancho, pajiza; hilo oblongo; embrión poco menos de ½ del largo de la cariopsis.

Distribución y ecología. Coleccionada unicamente en el estado de Paraná, Brasil (Fig. 8), donde habita en campos del NW del estado, a 1160 m.

Panicum magnispicula se asemeja a *P. chasei,* distingiéndose esta última por tener inflorescencias multifloras, pedicelos escabriúsculos y espiguillas de 2.8–3.8 mm de largo.

22. Panicum miliaceum L., Sp. Pl. 1: 58. 1753. *Milium panicum* Mill., Gard. Dict. (ed. 8): n. 1. 1768. *Milium esculentum* Moench, Methodus: 203. 1794. *Panicum milium* Pers., Syn. Pl. 1: 83. 1805, nom. illeg. superfl. *Leptoloma miliacea* (L.) Smyth, Trans. Kansas Acad. Sci. 25: 86. 1913. TIPO: India (lectótipo, designado por Sherif & Siddiqi (1988), no visto).

Plantas anuales, cespitosas, herbáceas, de 15–70 cm de alto. *Cañas* decumbentes, ramificadas o

no en los nudos inferiores, a erectas, ramificadas en los nudos superiores; entrenudos cilíndricos, huecos, pilosos, de 2–12 cm de largo; nudos oscuros, cubiertos de pelos blanquecinos. *Vainas* de 4–12 cm de largo, mayores que los entrenudos, estriadas, herbáceas, densamente pilosas, con pelos tuberculados caducos. *Lígulas* de 1–1.3 mm de largo, cortamente membranáceas en la base, luego largamente ciliadas. *Láminas* oblongo-lanceoladas, de 6–25 cm de largo, 0.4–1.2 cm de ancho, planas, de color verde oscuro, subcordadas en la base, con nervio medio manifiesto y bordes membranáceos, escabrosos, pilosas en ambas caras, los márgenes inferiores ciliados con pelos tuberculados. *Pedúnculos* cilíndricos, pilosos. *Inflorescencias* laxas, multifloras, nutantes, de 6–20 cm de largo, 4–11 cm de ancho, incluidas cuando jóvenes en las hojas superiores; *eje principal* triquetro, escabroso, ondulado, con largos pelos blanquecinos hacia la parte basal o sin los mismos; pulvínulos glabros, pajizos; ramificaciones alternas, raro subopuestas, divergentes del eje principal y desnudas en la porción basal, las espiguillas solitarias sobre largos pedicelos; pedicelos escabrosos, esparcidamente pilosos, de 4–9 mm de largo. *Inflorescencias axilares* similares a las inflorescencias terminales. *Espiguillas* ovoides, de 4.6–5.5 mm de largo, 1.5–2.1 mm de ancho, no estipitadas, glabras, pajizas, con tintes violáceos, gluma superior y lemma inferior subiguales, con nervios marcados y superando en largo al antecio superior. *Gluma inferior* de 2.8–3.6 mm de largo, ½ a ¾ del largo de la espiguilla, 5–7-nervia, el nervio medio escabriúsculo en su porción superior, de ápice atenuado. *Gluma superior* de 4–5.1 mm de largo, 11–13(–15)-nervia, el nervio medio escabriúsculo. *Lemma inferior* de 4–4.8 mm de largo, 11–13-nervia, glumiforme. *Pálea inferior* ovada, reducida, de 1.2–1.6 mm de largo, 0.5–0.8 mm de ancho, ½ o un poco menos del largo del antecio superior, membranácea, con el ápice bilobado. *Antecio superior* elipsoide, de 2.7–3.4 mm de largo, 1.3–1.9 mm de ancho, llegando cuando maduro a 2.3 mm de ancho, tempranamente caedizo, liso, glabro, lustroso, blanquecino, amarillento a la madurez, con dos cicatrices basales de ca. 0.4 mm de largo; lemma 7-nervia; pálea con papilas verrugosas junto al ápice. *Cariopsis* de 2–2.3 mm de largo, 1.4–1.8 mm de ancho, blanquecina; hilo punctiforme; embrión aproximadamente la mitad del largo de la cariopsis.

Distribución y ecología. Originaria del Viejo Mundo, donde es cultivada desde la antigüedad. Introducida en América, donde se cultiva para alimento de aves, como pequeño cereal, o para pastoreo de verano; es apreciada por su precocidad y resistencia a la sequía (Palacios, 1969).

Nombre vulgar. "Mijo."

Material representativo citado. ARGENTINA. **Buenos Aires**: Punta Lara, *Zuloaga 1890** (SI). **Distrito Federal**: sin localidad, *Calderón 1672* (BAA). **Cordoba**: Ascochinga, *Giardelli 616* (BAA, SI). **Corrientes**: Corrientes, *Quarín 1321* (CTES). **Entre Ríos**: Concepción del Uruguay, *Burkart 24109* (SI). **La Pampa**: Telen, *Monticelli 168* (SI). **La Rioja**: Chilecito, *Dawson 3355* (BAA). **Mendoza**: Godoy Cruz, *Rutz Leal 5576* (BAA, LIL). **Salta**: Salta, Chachapoyas, 14 ene. 1989, *Novara 8436* (M). **Santa Fe**: Rosario, Isla del Rowing, 6 ene. 1938, *Christian s.n.* (SI). **Tucumán**: Capital, calle lateral del Hipódromo, *Türpe 3009* (LIL). BRASIL. **Distrito Federal**: Plano Piloto, SQN 76, *Filgueiras 1204* (IBGE). **Rio Grande do Sul**: São Leopoldo, *Rambo 1937* (BAA). **Santa Catarina**: Rosario, *Reitz & Klein 17008* (US). **São Paulo**: Pinheiros, *Gehrt 31509* (US). COLOMBIA. **Valle**: Palmira, Estación Agrostológica, *Villamizar-Jaramillo s.n.* (COL-44878). ESTADOS UNIDOS DE AMERICA. **California**: Butte Co., on the S edge of Pentz Road, about 1 mile E of Highway 99, 10 Aug. 1988, *Ahart 6168* (MO). **Florida**: Pensacola, 8 Aug. 1901, *Curtiss 6867* (MO). **Massachusetts**: Dump Valley Road, Dorchester, 10 Sep. 1916, *Churchill 7* (MO). **Mississippi**: ca. 4 miles N of Biloxi along highway to Hattiesburg, 24 July 1971, *Lasseigne 2812* (MO). **Missouri**: St. Louis, Lindenwood freight yard of the Frisco Railroad, 3 July 1955, *Muelhenbach 667* (MO). **New York**: Ithaca, 21 Jul. 1916, *Metcalfe 5511* (MO). **North Dakota**: 18 miles S and 15 miles W of Fargo, 17 Aug. 1971, *Seiler 3825* (MO). **Utah**: North Park, Provo, *Mengies 8023* (MO). **Vermont**: Chittenden Co., Flagstaff, in yard of house at Rt. 3, 66 Leisure Lane, 29 Aug. 1983, *Ricketson 677* (MO). GUAYANA FRANCESA. Station des Nouragues, Bassion de l'Arataye, *Feuillet 4442* (US). HONDURAS. **Francisco Morazán**: El Zamorano, 800 m, *Rodríguez 3512* (US). REPUBLICA DOMINICANA. **Santo Domingo**: Santo Domingo, Jardín Botánico, *Liogier 21371* (NY).

Especie relacionada con *P. capillare* y *P. hirticaule*; la primera se distingue por tener inflorescencias erectas, caedizas, con espiguillas de 2–2.8(–3.2) mm de largo, y gluma superior y lemma inferior 7–9-nervias. *Panicum hirticaule* se separa por poseer inflorescencias erectas, con espiguillas cobrizas a violáceas, adpresas, de 1.9–2.8(–3.5) mm de largo, gluma superior y lemma inferior 7–9(–11)-nervias.

23. Panicum mohavense Reeder, Phytologia 71: 300. 1991. TIPO: Estados Unidos de América. Arizona: Mohave Co., Arizona strip, Main Street Valley, ca. 1.5 km S of the junction of the Colorado City road with the Main Street Valley road, low hills with limestone terraces, ca. 1525 m, 11 Oct. 1990, *Reeder & Reeder 8630**,** (holótipo, ARIZ no visto; isótipos, K no visto, MO, US-3238288). Figura 25 G–N.

Plantas anuales, de 2–6(–8) cm de alto, profu-

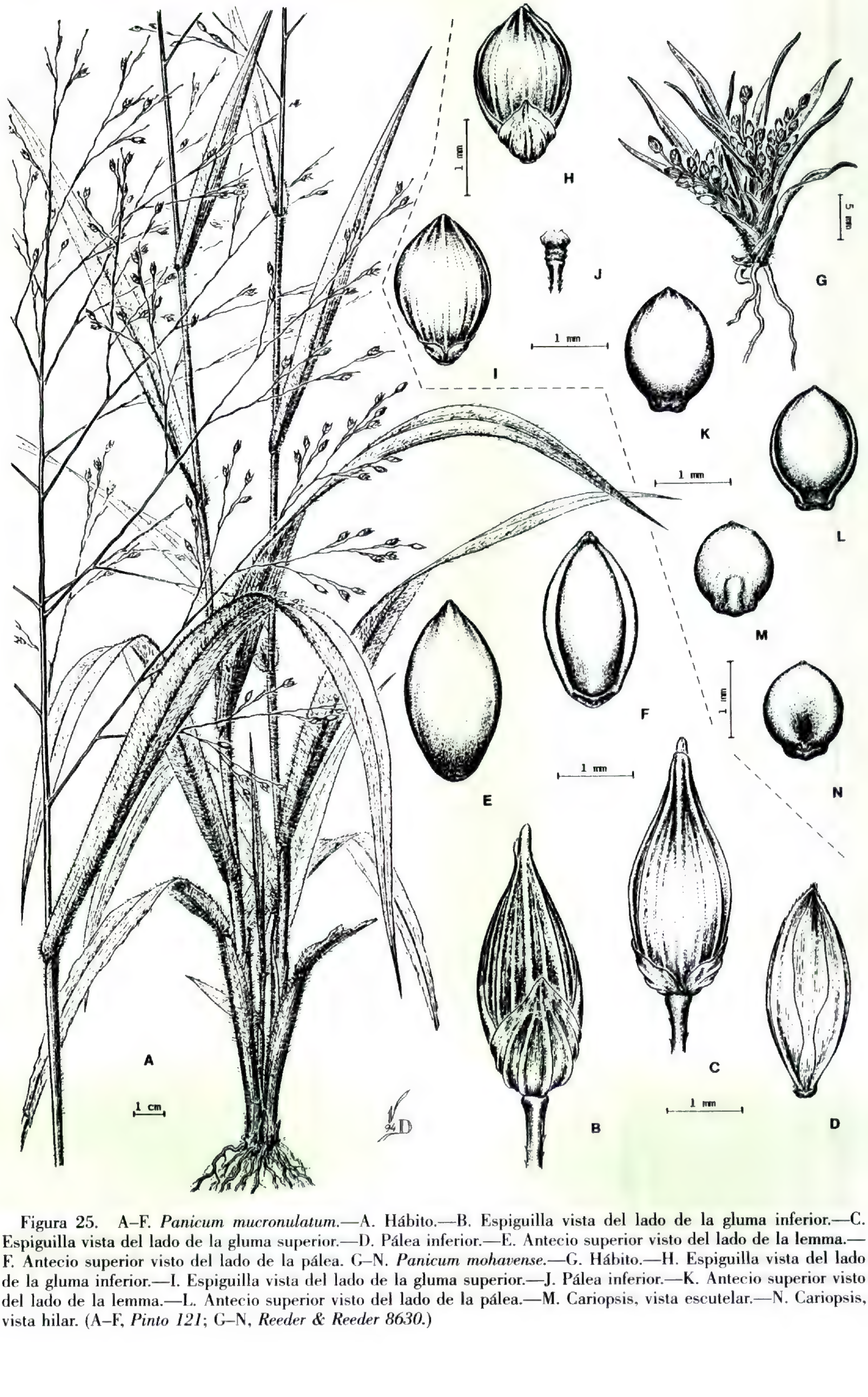


Figura 25. A–F. *Panicum mucronulatum.*—A. Hábito.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Pálea inferior.—E. Antecio superior visto del lado de la lemma.—F. Antecio superior visto del lado de la pálea. G–N. *Panicum mohavense.*—G. Hábito.—H. Espiguilla vista del lado de la gluma inferior.—I. Espiguilla vista del lado de la gluma superior.—J. Pálea inferior.—K. Antecio superior visto del lado de la lemma.—L. Antecio superior visto del lado de la pálea.—M. Cariopsis, vista escutelar.—N. Cariopsis, vista hilar. (A–F, *Pinto 121*; G–N, *Reeder & Reeder 8630.*)

samente ramificadas en la base. *Cañas* paucinodes, erectas; entrenudos 1–2, más cortos que las vainas foliares; nudos híspidos. *Vainas* de 0.4–1.5 cm de largo, estriadas, verdosas o con tintes violáceos, papiloso-híspidas en toda su superficie o hacia la porción basal, con los márgenes esparcidamente papiloso-pestañosos. *Lígulas* de 0.2–0.4 mm de largo, membranáceo-pestañosas, con largos pelos blanquecinos en la cara abaxial, hasta de 0.8 mm de largo; cuello glabro. *Láminas* linear-lanceoladas, de 1–4 cm de largo, 1–3 mm de ancho, erguidas, planas, glabras, de base recta, continuándose imperceptiblemente con la vaina y ápice agudo, los bordes basales papiloso-pestañosos, luego glabros, escabrosos, involutos hacia el ápice. *Pedúnculos* incluidos en las vainas foliares. *Inflorescencias* subespiciformes, paucifloras, subincluidas en las vainas foliares, no superando en largo a las hojas, 0.5–2 cm de largo, 0.5 cm de ancho; *eje principal* anguloso, escabriúsculo sobre las aristas; pulvínulos glabros; ramificaciones flexuosas, escabrosas; pedicelos de 0.5–2.8 mm de largo, escabrosos. *Espiguillas* globosas, de 2–2.3 mm de largo, 1–1.2 mm de ancho, glabras, de ápice cortamente acuminado, verde-pálidas o con tintes violáceos; gluma superior y lemma inferior subiguales, tan largas como la espiguilla. *Gluma inferior* ovada, de 0.8–1 mm de largo, de ápice obtuso a agudo, membranácea, delicada, abrazadora, 3-nervia. *Gluma superior* de 2–2.2 mm de largo, 9-nervia, con los nervios manifiestos, el central escabriúsculo hacia el ápice. *Lemma inferior* glumiforme, 9-nervia. *Pálea inferior* ausente o reducida, cuando presente hasta de 0.4 mm de largo, hasta ⅓ del largo del antecio superior, hialina, glabra. *Antecio superior* anchamente ovoide, de 1.4–1.8 mm de largo, 1 mm de ancho, alcanzando igual largo que la gluma superior y lemma inferior, pajizo, castaño claro a la madurez, lustroso, con un anillo y 2 pequeñas cicatrices en la base, castañas a la madurez; lemma 7-nervia; pálea con papilas simples junto al ápice; lodículas 2, ca. 0.4 mm de largo; estambres 3, las anteras de 0.9 mm de largo. *Cariopsis* anchamente elipsoide, de 1.3 mm de largo, 1 mm de ancho, olivácea; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Conocida sólo para el estado de Arizona en los Estados Unidos de América (Fig. 3), donde crece en campos abiertos a 1525 m.

Especie relacionada a *P. stramineum*, distinguiéndose esta última por incluir plantas mayores, hasta de 125 cm de alto, con láminas de 4.5–30(–42) cm de largo por 0.3–1.3(–2) cm de ancho, espiguillas de 2.3–3.2 mm de largo y pálea inferior tan larga o más larga que el antecio superior.

24. Panicum mucronulatum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 2. 1921. TIPO: Brasil. Bahia: sin localidad, *Blanchet 104* (lectótipo, aquí designado, B, isolectótipo, US-80776; probable isolectótipo, NY, foto del lectótipo, K). Figura 25A-F.

Panicum virgatum L. var. *pilosum* Döll in Martius, Fl. Bras. 2(2): 217. 1877. SINTIPOS: Brasil. Bahia: Ilheus, *Blanchet 2961* (K, MO, US). Pará: Almeirim, *Martius s.n.* (M no visto).

Plantas anuales, herbáceas, cespitosas. *Cañas* erectas de 60–100 cm de alto, ramificadas en los nudos inferiores, multinodes; entrenudos comprimidos, huecos, con largos pelos blanquecinos adpresos o con pelos tuberculados, erguidos; nudos oscuros, comprimidos, pilosos. *Vainas* comúnmente mayores que los entrenudos, pajizas, cubiertas de pelos tuberculados rígidos, quebradizos y urticantes, los bordes ciliados. *Lígulas* membranáceo-ciliadas, de 1.4–1.6 mm de largo, arqueadas; cuello densamente piloso, cubierto de pelos tuberculados. *Láminas* lanceoladas, de 25–45 cm de largo, 1–1.5 cm de ancho, planas, hirsutas, de ápice acuminado a subulado y base subcordada, los bordes ciliados a escabrosos, el nervio medio manifiesto. *Pedúnculos* parcialmente subincluidos en las vainas foliares, híspidos hacia la porción distal. *Inflorescencias* terminales exertas; panojas laxas, difusas, piramidales, multifloras, de 25–40 cm de largo, 10–30 cm de ancho; *eje principal* anguloso, hirsuto en la porción basal, luego escabroso, pulvínulos glabros; ramificaciones de primer orden alternas, raro opuestas, divergentes; eje de las ramificaciones hirsutos a escabrosos, las espiguillas difusas y regularmente dispuestas sobre la ramificaciones; pedicelos triquetros, escabrosos, de 2–20 mm de largo. *Espiguillas* solitarias, ovoides, de 3.3–3.6(–3.9) mm de largo, 1.3–1.6 mm de ancho, no estipitadas, glabras, verdosas o con tintes violáceos, glumas y lemma inferior con nervios marcados, subiguales, superando 1 mm en largo al antecio superior. *Gluma inferior* de 1.5–2 mm de largo, ½ del largo de la espiguilla, aguda, (3–)5–7-nervia, el nervio medio escabriúsculo, los nervios anastomosados hacia el ápice. *Gluma superior* aguda, de 2.8–3 mm de largo, 9–13-nervia. *Lemma inferior* glumiforme, 3–3.3 mm de largo, 7–9-nervia. *Pálea inferior* elíptica, de 2.3–2.6 mm de largo, 0.9–1.1 mm de ancho, membranosa, blanquecina, glabra, tan larga como el antecio superior, los bordes y el ápice esparcidamente pilosos. *Antecio superior* ovoide, de 2.2–2.4 mm de largo, 1–1.2 mm de ancho, glabro, pajizo, liso, lustroso, crustáceo, con dos cicatrices basales ca. 0.2 mm de largo; lemma 7-nervia; pálea con micropelos

globosos y papilas simples distribuidas irregularmente en su ápice. *Cariopsis* anchamente elipsoide, de 1.6 mm de largo, 1.1 mm de ancho; hilo punctiforme; embrión la mitad del largo de la cariopsis.

Distribución y ecología. Brasil, en los estados de Alagoas y Bahia (Fig. 4); se encuentra en bordes de arroyos o cerca de cultivos de caña de azucar, entre los 25 y 200 m.

Nombre vulgar. "Capim-de-orvalho."

Material adicional examinado. BRASIL. **Alagoas**: Porto Calvo, Fazenda Porto Seguro, *Campelo 2154* (CEN). **Bahia**: sin localidad, *Gardner 208* (US); Dom Macedo Costa, Fazenda Mocambo, 5 Mar. 1985, *Noblick & Lemos 3955* (CEPEC); Mun. Santo Antonio de Jesus, BR-101 Cruz das Almas-Itabuna, km 44, *Coradin et al. 3394* (CEN); 200 m, Cruz das Almas, *Pinto 121* (CEPEC), *306*,*** (IAN, US); Cachoeira, 25–50 m, coarse tufts, near streamlet, brushy border of sugar cane field, *Chase 8105** (NY, RB, US), *8105bis* (US); Municipio São Sebastião do Passé, Area da Estação Experimental Miranda, km 62 da Rod. BR 324, *Hage et al. 1716* (CEPEC, K). **Paraíba**: Escola do Agronomia do Nordeste, *Moraes 677** (SP, US). **Pernambuco**: Escola de Agronomia do Nordeste, *Coelho de Moraes 677* (IAN, SP); Recife, *Sendulsky 1434A* (SI, SP); Tapera, Apr. 1928, *Pickel 1393** (US); near Vitoria, W of Recife, *Davis & Andre-Lima 61068* (IBGE); sin localidad, *Gardner 1838* (K), *Glocker 208* (US).

Panicum mucronulatum es afín a *P. hispidifolium* y *P. stramineum*. *Panicum hispidifolium* se aparta por tener espiguillas globosas abiertas en el ápice, gluma superior y lemma inferior de igual largo que el antecio o hasta 0.3 mm más largo que el mismo, gluma superior 7-nervia y pálea inferior ¾ del largo del antecio superior. *Panicum stramineum* se distingue por tener inflorescencias con ramificaciones desnudas hacia la base, espiguillas globosas, de 2.3–3.2 mm de largo, gluma superior y lemma inferior de igual largo que el antecio superior o hasta 0.4 mm más largas.

25. Panicum pampinosum Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 66, fig. 48. 1910. *Panicum capillare* L. var. *pampinosum* (Hitchc. & Chase) Gould, Madroño 10: 94. 1949. *Panicum hirticaule* J. Presl var. *pampinosum* (Hitchc. & Chase) Beetle, Phytologia 47: 382. 1981. TIPO: Estados Unidos de América. Arizona: 2600 ft., Wilmot, 25 ago. 1903, *Thornber 193** (holótipo, US-592754; isótipo, MO-2752215).

Plantas anuales, de 11–27 cm de alto. *Cañas* erectas a ramificadas en los nudos basales y medios; entrenudos de 2–3 cm de largo, glabros, violáceos a pajizos; nudos pilosos, con pelos blanquecinos, sedosos, hasta de 1 mm de largo. *Vainas* de 1.5–2.5 cm de largo, usualmente más largas que los entrenudos, con tintes violáceos, papiloso-pilosas, con los márgenes pestañosos. *Lígulas* membranáceo-pestañosas, de 1 mm de largo; cuello glabro, blanquecino. *Láminas* linear-lanceoladas, de 3–5 cm de largo, 0.3 cm de ancho, ascendentes, erectas, poco divergentes, planas, cortamente pilosas en ambas caras, de base redondeada y ápice agudo, con los márgenes escabriúsculos, ondulados, los basales pestañosos, nervio medio blanquecino. *Pedúnculos* hasta de 4 cm de largo a subincluidos, cilíndricos, glabros, purpúreos. *Inflorescencias* largamente exertas, terminales, espiciformes a subespiciformes, de 5–6 cm de largo, 1–2 cm de ancho, paucifloras; *eje principal* triquetro, glabro, escabriúsculo; pulvínulos glabros; ramificaciones de primer orden 3–4(–5), alternas, las inferiores de 4–8 cm de largo, glabras, desnudas hacia la base; ramificaciones de segundo orden adpresas, con espiguillas próximas, apretadas sobre las ramas; pedicelos de 1–5 mm de largo, glabros, escabriúsculos. *Inflorescencias axilares* similares a la terminal, de menor tamaño, de 2–3 cm de largo. *Espiguillas* globosas, 3.6–4 mm de largo, 1.4 mm de ancho, túrgidas, no estipitadas, de ápice agudo, glabras, pajizas o con tintes violáceos; gluma superior y lemma inferior subiguales, superando 1.6 mm en largo al antecio superior. *Gluma inferior* ovado-acuminada, de 2.4–3.1 mm de largo, ⅘ del largo de la espiguilla, 3–5-nervia. *Gluma superior* de 3.6–4 mm de largo, 7-nervia, con los nervios verdosos. *Lemma inferior* glumiforme, de 3.2–3.5 mm de largo, 9-nervia. *Pálea inferior* reducida, de 0.7 mm de largo, 0.3 mm de ancho, ⅓ del largo del antecio superior, hialina, glabra. *Antecio superior* ovoide, de 2–2.4 mm de largo, 1.2 mm de ancho, túrgido, globoso, crustáceo, liso, lustroso, pajizo, con 2 cicatrices basales, ca. 0.3 mm de largo; lemma 7-nervia; pálea con papilas simples junto al ápice. *Cariopsis* no vista.

Distribución y ecología. Sur de los Estados Unidos de América y México (Fig. 10); crece en campos en áreas a menudo perturbadas entre 780 y 2250 m; florece entre agosto y octubre.

Material adicional examinado. ESTADOS UNIDOS DE AMERICA. **Arizona**: Greenlee County, about 40 miles N of Clifton along Coronado Trail, 7500 ft., 25 Aug. 1971, *Reeder & Reeder 5520* (US); Tucson Mountains, 25 Aug. 1904, *Griffiths 6939 1/2* pr. p. (US). **New Mexico**: Grant County, 1880–1881, *Rusby 444* (US); sin localidad, 1851–1852, *Wright 2084* (US); Organ Mountains, 29 Aug. 1894, *Wooton 2014* (US). MEXICO. **Chihuahua**: Miñaca, 7000 ft., 13 Oct. 1910, *Hitchcock 7751* (US).

Esta especie se caracteriza por incluir plantas de porte pequeño, con panojas espiciformes a subes-

piciformes y espiguillas globosas de 3.6–4 mm de largo, con gluma inferior $\frac{1}{5}$ del largo de la espiguilla.

Swallen (1955) cita esta especie para Guatemala en los departamentos de Chiquimula, Jutiapa y Zacapa, sin indicar los ejemplares de herbario correspondientes. No se han hallado espécímenes de dicho país por lo que esta cita se considera dudosa.

26. Panicum parcum Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 68, fig. 53. 1910. *Panicum decolorans* Kunth var. *parcum* (Hitchc. & Chase) Beetle, Phytologia 54: 4. 1983. TIPO: México. Sinaloa: Lodiego on the Culiacán River, mountain side, not very common, 9–15 Oct. 1981, *Palmer 1657*** (holótipo, US-471378; isótipos, F, ISC, NY, P).

Plantas anuales, cespitosas. *Cañas* erectas a geniculadas, de 20–90 cm de alto, simples, paucinodes, innovaciones extravaginales; entrenudos de 5–20 cm de largo, 2 mm diám., cilíndricos, glabros a hirsutos; nudos glabros, castaños. *Vainas* de 10–12 cm de largo, comúnmente más cortas que los entrenudos, hirsutas con pelos tuberculados, los márgenes pestañosos. *Lígulas* cortamente membranáceas en la base y luego largamente ciliadas, de 1–1.2 mm de largo; cuello hirsuto, castaño. *Láminas* linear-lanceoladas, de 6–45 cm de largo, 0.4–0.7 cm de ancho, planas, de base angostada, agudas, hirsutas, con pelos caducos, de base tuberculada, de aproximadamente 1 mm de largo, los bordes escabrosos, pestañosos hacia la base, el nervio medio manifiesto. *Pedúnculos* subincluidos en las vainas foliares a exertos, de 10–35 cm de largo, hirsutos en la porción distal. *Inflorescencias* terminales exertas, de 7–30 cm de largo, 6–15 cm de ancho, laxas, difusas, erectas; *eje principal* anguloso, escabriúsculo, glabro a hirsuto hacia la base; pulvínulos violáceos, glabros; ramificaciones de primer orden alternas, divergentes, las inferiores de 6–15 cm de largo; pedicelos triquetros, de 5–18 mm de largo, escabriúsculos, glabros. *Inflorescencias axilares* presentes, similares a las inflorescencias terminales. *Espiguillas* solitarias, ovoides, de 4.5–6 mm de largo, 1.8–2 mm de ancho, glabras, verdosas y con tintes violáceos, estipitadas; gluma superior y lemma inferior subiguales, 1.2–1.8 mm más largas que el antecio superior. *Gluma inferior* de 3–4.2 mm de largo, ¾ del largo de la espiguilla, aguda, 5–7-nervia, el nervio medio escabroso, separada por un entrenudo marcado de la gluma superior, ca. 0.6 mm de largo. *Gluma superior* de 3.9–5.4 mm de largo, 9–11-nervia, el nervio medio escabroso, cortamente escabrosa en la cara interna. *Lemma inferior* aguda, de 3.6–4.8 mm de largo, 9–11-nervia, escabrosa en la cara interna. *Pálea inferior* lanceolada, reducida, de 1.2–1.8 mm de largo, 0.4–0.6 mm de ancho, ½ o algo menor del largo del antecio superior, membranácea, glabra. *Antecio superior* ovoide, de 2.7–3.3 mm de largo, 1.5–2 mm de ancho, crustáceo, glabro, liso, lustroso, pajizo, con tintes negruzcos a la madurez, de base circular, castaña a la madurez; lemma 7-nervia; pálea con papilas verrugosas en el ápice. *Cariopsis* ovoide, de 2.3–2.5 mm de largo, 1.4–1.8 mm de ancho, blanquecina; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Se encuentra desde México hasta Costa Rica (Fig. 7), en terrenos rocosos abiertos o en bosques de pinos, entre el nivel del mar y 2070 m de elevación; florece entre julio y octubre.

Material representativo citado. COSTA RICA. **Guanacaste**: South end of Playas del Coco, 14 Nov. 1968, *Pohl & Davidse 11437* (F, US). GUATEMALA. **Chiquimula**: grassy plains and low slopes around Chiquimula, 400 m, 20 Oct. 1939, *Steyermark 30064* (F, US). **Jutiapa**: region of El Tablón, northeast of Jutiapa, 850-900 m, 31 Oct. 1940, *Standley 75925* (F, US); vicinity of Jutiapa, 850 m, 24 Oct. 1940, *Standley 75102a* (F, US). **Zacapa**: near La Fragua, 200–500 m, 14 Oct. 1940, *Standley 74761* (F, US); rocky hills in vicinity of Santa Rosalía, 2 mi. south of Zacapa, 200 m, 7 Oct. 1939, *Steyermark 29310* (F). HONDURAS. **El Paraíso**: Road to Yuscarán, edge of brushy places, 800 m, 5 Nov. 1951, *Swallen 11371* (MO, US); road to Danlí, not far from Río Choluteca, *Swallen 11250* (US). **Francisco Morazán**: region of Las Mesas, pine hills around the Zamorano valley, rocky pine woods, 800–900 m, 2 Nov. 1951, *Swallen 10765* (MO, US); San Antonio del Oriente, 1200 m, *Swallen 10909* (US). MEXICO. **Chiapas**: 14 km E of Ocozocuatla, in open grassy field, *Gould 12729** (MO, US); 9 km north of Tuxtla Gutiérrez, along road to El Sumidero, 2500 ft., 27 Oct. 1965, *Breedlove & Raven 13833* (F, MEXU, US). **Chihuahua**: Río Negro, 28 ago. 1937, *Le Sueur 173* (US). **Colima**: Alzada, *Hitchcock 7081* (RB, US). **Durango**: 14 mi. SE of Durango, about 600 ft., 16 Oct. 1966, *Gould 12288* (US). **Guanajuato**: km 20 N de Silao, 16 sep. 1946, *Hernández Xolocotzi et al. X-2468* (US). **Guerrero**: Balsas, *Hitchcock 6782* (F, MO, NY, US); Coyuca, Santa Barbara, 29 Sep. 1934, *Hinton 6686* (GH, MO, NY, US). **Jalisco**: about 13 miles northwest of León, Guanajuato in a grassy area with scattered thorny shrubs, 2070 m, *Reeder & Reeder 2288* (US). **Michoacán**: West-facing slopes of Cerro de Carboneras, ca. 22 km S of Uruapan, 3300-3700 ft., *King & Soderstrom 4831* (MEXU, NY, US). **Morelos**: Xochiltepec, 24 Sep. 1938, *Lyonnet 2639* (MEXU, MO, US). **Nayarit**: Mun. Nayar, 3.9 km al NE de Jesús María, camino a Huejuquilla, 22°16′N, 104°30′W, 530 m, selva baja caducifolia, 15 sep. 1989, *Flores et al. 1053* (MO). **Oaxaca**: 11 mi. W of Zanatepec, 150 m, 28 Aug. 1953, *Reeder & Reeder 2152* (US); near km post 184 on Hwy. 190, ca. 40 miles NW of Tehuantepec, 710 m, 13 Aug. 1975, *Davidse 9587* (MO). **Puebla**: Mesa del Pochote 3 km al E de El Salado, bosque de Quercus, 1310 m, 20 oct. 1985, *Gutzar 1850* (ANSM, CHAPA). **Sinaloa**: Las

Mesas, Sierra Surotato, ca. 3000 ft., 15 Sep. 1941, *Gentry 6667* (GH, MO, NY). **Sin Estado**: Alzada, 4 Oct. 1910, *Orcutt 4687* (US). NICARAGUA. **León**: along Hwy. 12, 2 km SE of Jct. with Puerto Somoza road, 40 m, 8 July 1971, ca. 12 km E of Puerto Somoza, *Pohl 12707* (F, MO, NY); El Velero, at mouth of Estero San José, ca. 10 km by road S of Hwy. 32, 12°08′N, 86°45′W, 9 Sep. 1984, *Stevens 23096* (MO, SI). **Managua**: Inst. Pedagógico de Varones, *Vernier 1505* (GH).

Beetle (1977) considera a *P. parcum* como sinónimo de *P. decolorans*. Esta especie se distingue de *P. decolorans* por tener panojas laxas con las ramificaciones divergentes del raquis y espiguillas estipitadas, con gluma inferior y superior separadas por un entrenudo marcado.

27. Panicum peladoense Henrard, Blumea 4: 504. 1941. TIPO: Paraguay. Paraguarí: Cerro Pelado, 3 abr. 1883, *Balansa 4357*** (holótipo, L no visto; isótipos, G, K, MO, P, US-1108609, 1647868, 1649644). Figura 26.

Panicum campestre Nees, Fl. Bras. Enum. Pl. 2: 197. 1829, non Nees ex Trin., 1826. *Panicum cayennense* Lam. var. *campestris* (Nees) Pilg., Bot. Jahrb. Syst. 30: 132. 1901. TIPO: Brasil. São Paulo: entre Taubaté y Pindamonhangaba, *Martius s.n.* (holótipo, M, fragmento y foto, US-80546, fragmento, US-974750).

Panicum bergii Arechavaleta var. *leiophyllum* Hackel & Lindman, Kongl. Svenska Vetenskapsakad. Handl. 34 (6): 10, pl. 4b, 1900. TIPO: Brasil. Rio Grande do Sul: Cachoeira, 11 Feb. 1893, *Lindman 1185* (isótipos, P, US-702326, W).

Plantas perennes, cespitosas, de 20–60 cm de alto. *Cañas* erguidas, simples, paucinodes; entrenudos de 3.5–10.5 cm de largo, cilíndricos, huecos, densamente híspidos a glabrescentes; nudos violáceos y con pelos blanquecinos densa a esparcidamente dispuestos. *Vainas* de 3.5–8 cm de largo, usualmente menores que los entrenudos, pajizas, densamente pilosas, con pelos adpresos de base tuberculada a glabrescentes, los bordes ciliados. *Lígulas* cortamente membranáceas y luego largamente ciliadas, de 0.5–1.7 mm de largo; cuello castaño claro, piloso. *Láminas* lanceoladas a linear-lanceoladas, de 7–22 cm de largo, 0.2–0.4 cm de ancho, erectas, ascendentes, planas, de base angostada continuándose imperceptiblemente con la vaina, densamente pilosas, con pelos tuberculados en ambas caras o sólo en la cara abaxial a glabras, los márgenes escabriúsculos y largamente ciliados, cartilaginosos. *Pedúnculos* subincluidos en las vainas foliares a exertos, hasta de 30 cm de largo, cilíndricos, glabros. *Inflorescencias* laxas, difusas, piramidales, de 7–18 cm de largo, 3–13 cm de ancho; *eje principal* cilíndrico, escabroso, con largos pelos esparsos o sin los mismos; pulvínulos glabros; ramificaciones alternas u opuestas, en ocasiones subverticiladas hacia la base, ramas escabrosas a pilosas; pedicelos glabros, claviformes, escabrosos, de 2–20 mm de largo. *Espiguillas* largamente ovoides, acuminadas, de (2.5–)2.7–3.3(–3.7) mm de largo, 1–1.2 mm de ancho, solitarias, no estipitadas, glabras, pajizas, con tintes violáceos; gluma superior y lemma inferior subiguales y superando 1–1.2 mm en largo al antecio superior. *Gluma inferior* ovada, aguda, de (1.5–)1.7–2.1(–2.4) mm de largo, ½ a ¾ del largo de la espiguilla, 5–7-nervia, el nervio medio escabriúsculo hacia la porción superior. *Gluma superior* de (2.3–)2.6–3.1(–3.4) mm de largo, 7–9-nervia, caduca a la madurez de la espiguilla y dejando al descubierto el dorso de la lemma superior, la cara interna escabriúscula hacia el ápice; gluma inferior y superior separadas por un entrenudo ca. 0.3 mm de largo. *Lemma inferior* glumiforme, de 2.5–3(–3.4) mm de largo, 7–9-nervia. *Pálea inferior* elíptica, de 1.7–2.2 mm de largo, 0.6–0.9 mm de ancho, tan larga como el antecio superior, membranácea, hialina, con los bordes finamente pilosos a glabros, de ápice bilobado a entero. *Antecio superior* elipsoide, de (1.7–)1.9–2.1 (–2.3) mm de largo, 0.8–1.1 mm de ancho, crustáceo, glabro, liso, lustroso, pajizo, negro a la madurez, con dos cicatrices basales ca 0.1 mm de largo; lemma 7-nervia; pálea con papilas simples hacia el ápice. *Cariopsis* de 1.2–1.3 mm de largo, 0.6–0.9 mm de ancho; hilo punctiforme; embrión ⅓ del largo de la cariopsis.

Distribución y ecología. Habita en campos de Argentina, Bolivia, Brasil, Paraguay y Uruguay (Fig. 4); llega hasta los 1200 m. Florece de octubre a marzo.

Material representativo citado. ARGENTINA. **Córdoba**: 7 km W de Sta. Rosa de Calamuchita, *Quarín 2909* (CTES, SI, US). Sin localidad, 9 ene 1919, *Castellanos 43** (F, SI, US). **Corrientes**: Dpto. Capital, Ruta 12, Riachuelo, *Eskuche 2538-5** (SI); Río Paraná near Arroyo Sombrero, 27 Feb. 1978, *Renvoize et al. 3637* (K, MO, NY, P, SI, US). **Jujuy**: Dpto. Capital, Sierra de Zapla, Mina 9 de Octubre, *Zuloaga & Deginani 137, 3447** (SI). **Misiones**: Dpto. Apóstoles, Apóstoles, *Martínez Crovetto 8978* (BAA). BOLIVIA. **Santa Cruz**: Florida, 10 km E of Samaipata, *Renvoize et al. 4044* (K); Cordillera, 50 km S of Santa Cruz, *Renvoize et al. 3933* (K). BRASIL. **Distrito Federal**: Reserva Ecologica do IBGE, *Filgueiras 1060** (SI, SP); Area da FAL, 5 mayo 1991, *Azevedo & Filgueiras 950* (MO). **Goiás**: between Viannápolis and Ponta Funda, open clay, sandy cerrado, *Chase 11280* (US). **Mato Grosso**: Santa Rita do Araguaya, on Rio Araguaya, *Chase 11858*; (US). **Mato Grosso do Sul**: Porto Esperança on Río Paraguay, *Chase 11071** (US); Campo Grande, 7 Feb. 1930, *Chase 10780** (US), between Campo Grande and Dourados, 400–500 m, 14–17 Feb. 1930, *Chase 10886* (F, US). **Minas Gerais**: Serra do Cipó, 110 km NE of Belo Horizonte, W of Vaccaria, 800 m, 28 Mar. 1925, *Chase 9279* (F, GH, MO, NY, US); Serra do Man-

Figura 26. *Panicum peladoense.*—A. Hábito.—B. Espiguilla, vista lateral.—C. Espiguilla vista del lado de la gluma inferior.—D. Espiguilla vista del lado de la gluma superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Antecio superior maduro.—I. Cariopsis, vista escutelar.—J. Cariopsis, vista hilar. (*Zuloaga & Deginani 137.*)

tiqueira, between Sitio and Dr. Sá Fortes, 1200 m, 1 Mar. 1925, *Chase 8696* (F, GH, K, MO, NY, US). **Pará**: Lagoa Aura Preta, *Drouet 1953* (F). **Paraná**: Mun. Arapoti, Campo Cerrado by Jaguariaíva boundary, *Smith et al. 14726* (K, NY, P, RB, US). **Rio Grande do Sul**: Alto do Morro da Gloria, Porto Alegre, *Valls & Arzivenco 2033* (CEN); Pelotas, 22 Apr. 1946, *Swallen 9156** (US). **Santa Catarina**: 17 km NE of the S. Catarina-RGS border, BR-116, *Davidse et al. 11145* (MO, NY, SP). **Sâo Paulo**: Fazenda Campininha, 10 km NEE of Padua Sales, 22°11'S, 47°10'W, 15 July 1960, *Eiten et al. 2116* (F, G, NY, US). **Sin Estado**: sin localidad, *Riedel 2155* (K), *Burchell 6794-2* (K), *Sellow s.n.* (K). PARAGUAY. **Amambay**: in altiplanitie Sierra de Amambay, *Hassler 12099* (G). **Concepción**: San Salvador, *Rojas 2784* (BAA, US). **Guairá**: praderas de Itaigú, près de Villa Rica, 17 dic. 1876, *Balansa 13* (BAF, G, K, P, US). **Paraguarí**: Cerro Peró, près de Paraguarí, 29 oct. 1876, *Balansa 14* (G, K, P, US). URUGUAY. **Rivera**: Estancia Ripol, ruta 5 próximo a ruta 29, *Del Puerto 1527* (P). **Tacuarembó**: Tacuarembó, Gruta de los Cuervos, 8 feb. 1981, *Cabrera & Zuloaga 32385* (SI), *32388** (MO, SI, US).

Henrard (1941) menciona en la descripción original de la especie que la misma posee vainas, nudos y láminas glabrescentes o con pilosidad rala. Se ha comprobado que el carácter de la pilosidad es variable, encontrándose desde ejemplares densamente pilosos hasta glabrescentes.

Esta especie fue descrita por Nees en 1829 como *P. campestre,* estando este nombre invalidado por existir un homónimo anterior descrito por Trinius en 1826, perteneciendo esta última especie a la sección *Rudgeana* (Zuloaga, 1987b). Henrard (1941) erróneamente señala que *P. campestre,* descrito por Nees en 1829, corresponde a *P. ghiesbreghtii.*

Una especie afín a *P. peladoense* es *P. exiguum* Mez, distinguiéndose esta última por ser una planta anual, con cañas abundantemente ramificadas y decumbentes en la base, con gluma inferior ¾ o más del largo de la espiguilla.

Panicum peladoense se separa de *P. chasei* por incluir el último taxon plantas con panojas espiciformes a subespiciformes, con espiguillas anchamente ovoides y antecio superior castaño a grisáceo a la madurez, sin la gluma superior caediza.

28. Panicum philadelphicum Bernhardi ex Trinius, Gram. Panic.: 216. 1826. *Panicum philadelphicum* Nees, Fl. Bras. Enum. Pl. 2: 198. 1829, hom. illeg. TIPO: "misit. s.n., Pan. philadelphici sibi cl. Bernhardi" (holótipo, LE no visto, fragmento y foto de tipo US-80910).

Panicum capillare L. var. *sylvaticum* Torrey, Fl. N. Middle United States: 149. 1824, non *P. sylvaticum* Lam., 1798. *Panicum torreyi* E. Fourn. in Hemsl., Biol. Centr.-Amer., Bot. 3: 497. 1885. TIPO: Estados Unidos de América. New York: "in dry woods near New York" (holótipo, UMO no visto, fragmento y foto US-80555).

Panicum capillare L. var. *campestre* Gattinger, Tennessee Fl.: 94. 1887, non *Panicum campestre* Nees, 1826. *Panicum capillare* L. var. *gattingeri* Nash, Ill. Fl. N.U.S. 1: 123. 1896, hom. illeg. superfl. *Panicum gattingeri* Nash in Small, Fl. S.E.U.S.: 92, 1327. 1903. TIPO: Estados Unidos de América. Tennessee: near Nashville, Sep., *Gattinger s.n.* (lectótipo, designado por Hitchcock & Chase (1910), TENN no visto, fragmento y foto US-80667).

Panicum capillare L. var. *minimum* Engelmann ex Gattinger, Tennessee Fl. 94. 1887. *Panicum minimum* (Engelm. ex Gatt.) Scribn. & Merr., U.S.D.A. Div. Agrostol. Circ. 27: 4. 1900. TIPO: Estados Unidos de América. Tennessee: "Green Brier, Sept. 1878, *Gattinger s.n.*" (lectótipo, designado por Hitchcock & Chase (1910), TENN no visto, fragmento US-80911).

Panicum capillare L. var. *geniculatum* Scribner. *in* Kearney, Bull. Torrey Bot. Club 20: 477 y 479. 1893, *non Panicum geniculatum* Lam. 1798. TIPO: Estados Unidos de América. Kentucky: Bell County, collected near Wasioto, Sep. 1894, Kearney Jr. 378 (lectótipo designado por Hitchcock & Chase, 1910, US-823622).

Panicum tuckermani Fernald, Rhodora 21: 112. 1919. *Panicum philadelphicum* Bernh. ex Trin. var. *tuckermani* (Fernald) Steyerm. & Schmoll, Rhodora 41: 90. 1939. TIPO: Vermont: head of Lake Memphremagog, Sep. 1859, *Tuckerman s.n.* (holótipo, GH, fragmento US-81287; isótipo, MO).

Panicum lithophilum Swallen, Proc. Biol. Soc. Wash. 54: 43. 1941. TIPO: Estados Unidos de América. Georgia: Stone Mountain, rocky slope, 23 Aug. 1905, *Hitchcock s.n., Amer. Gr. Nat. Herb. no 24* (holótipo, US-952898; isótipos, US-1912007, 2488400).

Plantas anuales, cespitosas, de 10–60 cm de alto. *Cañas* erectas, delicadas, ramificadas hacia la porción basal y media, menos frecuentemente decumbentes, arraigadas en los nudos basales; entrenudos de 2–5 cm de largo, 0.1 cm diám., hirsutos en toda su extensión o sólo hacia la porción superior; nudos pilosos. *Vainas* usualmente más largas que los entrenudos, de 2.5–7 cm de largo, verdes a púrpuras, híspidas, con pelos tuberculados, blanquecinos, hasta de 5 mm de largo, un borde pestañoso, el restante glabro. *Lígulas* membranáceo-pestañosas, de 0.8–1.3 mm de largo; cuello piloso. *Láminas* linear-lanceoladas, de 4–12 cm de largo, 0.2–0.6 cm de ancho, ascendentes, erectas, poco divergentes, planas, hirsutas a esparcidamente pilosas, verdes o con tintes purpúreos, de base redondeada a subcordada y ápice agudo, los bordes escabriúsculos, los inferiores largamente pestañosos, con pelos tuberculados, blanquecinos, de 0.6–3 mm de largo, el nervio medio hirsuto. *Pedúnculos* largamente exertos, hasta de 18 cm de largo, glabros a hirsutos junto al ápice, cilíndricos. *Inflorescencias* terminales laxas, difusas, de 7–27 cm de largo, 4–24 cm de ancho; *eje principal* glabro

a esparcidamente piloso hacia la porción basal, finamente escabriúsculo hacia la porción distal; pulvínulos glabros a cortamente pilosos; ramificaciones de primer orden alternas a subopuestas, divergentes, las inferiores de 7–15 cm de largo; ramificaciones de segundo orden divergentes; ramificaciones capiliformes, desnudas hacia la base, llevando 1–4 espiguillas; pedicelos cortos, de 0.3–1.5 cm de largo, adpresos, capiliformes, glabros, escabriúsculos. *Inflorescencias axilares* presentes. *Espiguillas* elipsoides, de 1.6–2.1 mm de largo, 0.5–0.7 mm de ancho, de ápice acuminado, no estipitadas, verdosas o con tintes violáceos; gluma superior y lemma inferior subiguales, tan largas como el antecio superior. *Gluma inferior* ovada, de 0.5–0.9 mm de largo, abrazadora, ½ o un poco menor del largo de la espiguilla, de ápice acuminado a redondeado, 3–5-nervia. *Gluma superior* de 1.6–2 mm de largo, 7-nervia. *Lemma inferior* de 1.6–1.9 mm de largo, 7–9-nervia. *Pálea inferior* ausente. *Antecio superior* angostamente elipsoide, de 1.5–1.7 mm de largo, 0.4 mm de ancho, crustáceo, pajizo, lustroso, con tintes negruzcos a la madurez, con un anillo circular en la base; lemma 7-nervia; pálea con papilas simples junto al ápice. *Cariopsis* elipsoide, de 1 mm de largo, 0.4 mm de ancho, pajiza; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Habita en los Estados Unidos de América (Fig. 3), sobre suelos graníticos en bosques abiertos o campos; florece entre abril y septiembre.

Material representativo citado. ESTADOS UNIDOS DE AMERICA. **Alabama**: Cullman Co., 8 Sep. 1897, *Eggert 58* (US). **Arkansas**: Saline Co., Ouachita Region, 9 Aug. 1971, *Demaree 64207* (MO). **Connecticut**: Franklin, 12 Sep. 1911, *Woodward s.n.* (US-1038355). **District of Columbia**: Deanwood, 12 Aug. 1905, *Chase s.n.* (MO). **Georgia**: Putnam Co., 13 mi. E of Eatonton, 19 Aug. 1940, *McVaugh 5164* (MO, US). **Kentucky**: Marion Co., 10 Aug. 1939, *Wharton 5151* (US). **Maryland**: Prince Georges Co., Ammendale, 15 Sep. 1916, *Hyacinth 960* (MO). **Massachusets**: Randolph, Punkapag Pond, 5 Sep. 1898, *Churchill 103* (MO). **Missouri**: 5 mi. E of Lebanon, upland woods bordering Mill Creek, 23 Aug. 1937 *Steyermark 25209* (MO); Maries Co., upper slopes along Gasconade River, 2½ mi. NE of Vienne, 29 Aug. 1937, *Steyermark 2554* (MO). **New Hampshire**: Sullivan Co., Unity, 20 Aug. 1963, *Seymour 20900* (MO). **North Carolina**: Polk Co., 1 mi. NW of Colombus, *Freeman 53433*** (US). **Oklahoma**: Sapulpa, 21 Sep. 1894, *Bush 722* (US); Muskogge, 18 Apr. 1940, *Bebb 5796* (US). **Pennsylvania**: Lancaster Co., in a swamp two miles S of Refton in Eozoic, 23 Sep. 1901, *Heller s.n.* (MO-2975482). **South Carolina**: Orangeburg, 16 Aug. 1905, *Hitchcock 7* (US). **Tennessee**: 3 mi. of Wolf Creek Station, 26 Aug. 1897, *Kearney Jr. 961* (MO, US); Montgomery Co., near Warfield, *Brown & Clebsch 569*,** (US). **Texas**: Dallas Co., *Reverchon 1842* (MO). **Vermont**: Caledonia Co., Kirby Mt., Kirby, 14 Aug. 1964, *Seymour 21936* (MO). **Virginia**: Portsmouth, 26 Aug. 1912, *Noyes 459* (MO). **West Virginia**: sin localidad, 11 Sep. 1903, *Steele & Steele 16* (MO). **Wisconsin**: Lincoln County, common in the Fire Lane, 30 Aug. 1955, *Seymour & Jones 16381* (MO).

Swallen diferencia a *Panicum lithophilum* de *P. philadelphicum* por poseer inflorescencias rígidas, con espiguillas de mayor tamaño, agrupadas en pares sobre el extremo de las ramificaciones y por tener hojas angostas, erectas y de color purpúreo. El examen de material de *P. philadelphicum* permitió comprobar que estos caracteres no son válidos para mantener a *P. lithophilum* como una entidad separada de *P. philadelphicum*.

Panicum philadelphicum está relacionado a *P. capillare* y *P. flexile*, separándose por poseer espiguillas acuminadas de 1.6–2.1 mm de largo, alcanzando el antecio superior igual largo que la gluma superior y la lemma inferior, con inflorescencias no caedizas y de forma piramidal (con panojas caedizas en *P. capillare* y angostamente elipsoides en *P. flexile*).

Ocasionalmente se observan en esta especie ejemplares con cañas decumbentes y arraigadas en los nudos inferiores, carácter señalado por Fairbrothers (1953).

29. Panicum quadriglume (Döll) Hitchcock, Contr. U.S. Natl. Herb. 24: 460. 1927. *Panicum cayennense* Lam. var. *quadriglume* Döll, in Martius, Fl. Bras. 2 (2): 220. 1877. TIPO: Brasil. Minas Gerais: Caldas, 18 Mar. 1887, *Regnell III-1406* (holótipo, W; isótipo, P, US-724411, fragmento, US-80560). Figura 27.

Plantas perennes, cespitosas, de 15–80 cm de alto. *Cañas* erectas, paucinodes, ramificadas hacia los nudos medios; entrenudos de 4–10 cm de largo, cilíndricos, cubiertos de pelos de base tuberculada a glabrescentes; nudos pajizos, cubiertos de largos pelos blanquecinos. *Vainas* menores que los entrenudos, de 3–9 cm de largo, densa a esparcidamente hirsutas, con pelos tuberculados, los bordes pestañosos. *Lígulas* de 0.5–1 mm de largo, con la base cortamente membranácea, luego ciliadas; cuello pajizo, glabro a piloso. *Láminas* linear-lanceoladas, de 6–26 cm de largo, 0.3–0.6 cm de ancho, erectas, ascendentes, rígidas, planas, de base angostada y ápice acuminado, densa a esparcidamente hirsutas en ambas caras con pelos tuberculados caducos, los bordes escabrosos y ciliados, con pelos tuberculados caducos. *Pedúnculos* subincluidos en las vainas foliares a exertos, de 8–20 cm de largo, cilíndricos, glabros. *Inflorescencias* terminales exertas, laxas, difusas, piramidales, de 7–20 cm

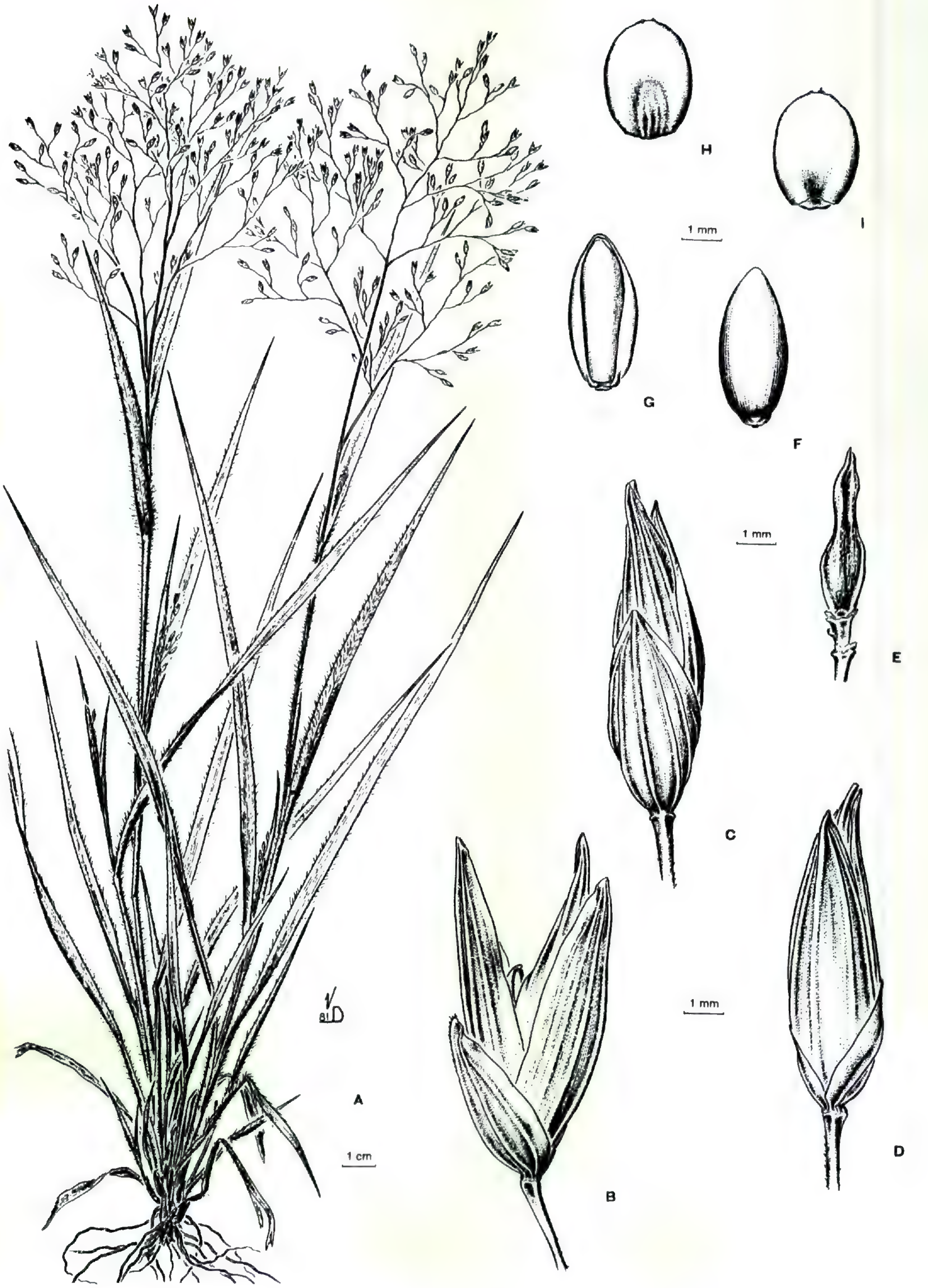


Figura 27. *Panicum quadriglume.*—A. Hábito.—B. Espiguilla, vista lateral.—C. Espiguilla vista del lado de la gluma inferior.—D. Espiguilla vista del lado de la gluma superior.—E. Pálea inferior.—F. Antecio superior visto del lado de la lemma.—G. Antecio superior visto del lado de la pálea.—H. Cariopsis, vista escutelar.—I. Cariopsis, vista hilar. (*Steinbach 6979.*)

de largo, 3–13 cm de ancho, cuando jovenes incluidas en las vainas superiores; *eje principal* glabro, triangular y escabriúsculo; pulvínulos glabros; ramificaciones de primer orden alternas, raro subopuestas o verticiladas hacia la parte superior, divergentes del raquis, escabrosas; pedicelos escabriúsculos, verdosos a violáceos, de 3–13 mm de largo. *Inflorescencias axilares* presentes, similares a las inflorescencias terminales. *Espiguillas* solitarias, largamente ovoides, acuminadas, de 2.5–4.2 mm de largo, 1–1.4 mm de ancho, no estipitadas, glabras, verdosas y con tintes violáceos, trifloras, con dos lemmas inferiores, una con y la restante sin su correspondiente pálea, y antecio superior con el dorso de la lemma dispuesto hacia la gluma inferior. *Gluma inferior* de 1.2–2.3 mm de largo, ½ del largo de la espiguilla, de ápice agudo a obtuso, 5–9-nervia, el nervio medio escabriúsculo hacia la porción superior. *Gluma superior* de 1.9–3.6 mm de largo, de ápice agudo a obtuso, caediza a la madurez, 7–9-nervia, el nervio medio escabriúsculo; gluma inferior y superior separadas por un corto entrenudo ca. 0.2 mm de largo. *Lemma inferior I* de 2.2–3.7 mm de largo, acuminada, 5–9-nervia. *Pálea inferior I* ausente. *Lemma inferior II* de 2.2–3.8 mm de largo, acuminada, 7–9-nervia. *Pálea inferior II* elíptica, de 1.5–2.3 mm de largo, 0.7–0.9 mm de ancho, tan larga como el antecio superior, membranácea, hialina, de ápice bilobado, brevemente ciliada o no hacia los bordes superiores, encerrando una flor estaminada. *Antecio superior* angostamente ovoide, de 1.6–2.3 mm de largo, 0.8–1.2 mm de ancho, 0.3–0.9 mm más corto que el largo de la espiguilla, crustáceo, glabro, liso, lustroso, pajizo, negro a la madurez, con dos cicatrices basales ca. 0.1 mm de largo, castañas a la madurez; lemma 7-nervia; pálea con papilas simples junto al ápice. *Cariopsis* anchamente elipsoide, de 1.6 mm de largo, 1–1.1 mm de ancho, pajiza; hilo punctiforme; embrión la mitad o más del largo de la cariopsis.

Distribución y ecología. Argentina, Bolivia, Brasil y Paraguay (Fig. 8). Habita en campos. Llega hasta los 2600 m; florece y frucitifica entre enero y mayo.

Material representativo citado. ARGENTINA. **Misiones**: Dpto. Montecarlo, Colonia Montecarlo, *Schwindt 1154* (LIL, MO, US). BOLIVIA. **Beni**: Near Reyes, 300 m, Apr. 1947, *Cutler 9084* (F, US). **La Paz**: Yungas, 1890, *Bang 493** (F, G, K, M, US); Inquisivi, climb between the Río Khara Bridge, ca. 3–4 km Licoma Pampa, 16°48′S, 67°14′W, 2600 m, 12 Mar. 1989, *Lewis 35344* (MO, SI). **Santa Cruz**: Ñuflo de Chávez, Comunidad Puesto Nuevo, 60 km of Concepción 16°25′S, 62°00′W, 450–750 m, 21 Feb. 1986, *Killeen 1828* (F, SI); Buena Vista, *Steinbach 6979* (BAA, F, G, GH, K, MO, US, W). BRASIL. **Goiás**: Goyandira, 800 m, campo, *Chase 11560** (RB, US); Mun. Presidente Kennedy, 12 km west of village of Presidente Kennedy, 3°25′S, 48°37′W, 1 Feb. 1980, *Plowman et al. 8226* (MO, NY). **Maranhao**: Grajahú to Porto Franco, *Swallen 3844* (IAN, K, RB, US). **Mato Grosso**: between Rondonópolis and São Lourenço, 16°20′S, 54°30′W, *Chase 11924* (US). **Mato Grosso do Sul**: vicinity of Dourados, 22°S, 54°30′W, 400 m, 18-21 Feb. 1930, *Chase 10976** (F, GH, MO, NY, US); Campo Grande, *Chase 10866** (R, US). **Minas Gerais**: Serro do Curral, SE of Belo Horizonte, trail to Pico, 1000 m, 26 Mar. 1925, *Chase 9089* (F, GH, MO, NY, US); Antonio Justiniano, 17 km S of Oliveira, 900 m, 16 Mar. 1925, *Chase 8897*,** (F, GH, MO, NY, RB, US, W). PARAGUAY. **Amambay**: Pedro Juan Caballero, *Rojas 12741* (LIL, MO); in regione calcarea cursus superioris fluminis Apa, *Hassler 10967* (BAF, G, K, NY, P, US). **Concepción**: entre el Río Apa y el Río Aquidabán, *Fiebrig 5102* (F, GH, M). **Cordillera**: Fortín Lopez, *Hassler 1942* (BAA, G, K, NY, P); región del lago Ipacaray, *Hassler 12494* (BAA, F, GH, K, MO, NY, US). **Paraguarí**: cerca de Sapucay, *Hassler 13022* (US). PERU. **Cajamarca**: valley of Río Tabaconas, 05°19′S, 79°14′W, 1700 m, 11 Apr. 1947, *Fosberg 27768* (US). **Cuzco**: bajando a Chavares, *Vargas 17225* (US). **Huancavelica**: entre Quintabamba y Virgen Pampa, 1200 m, *Tovar 4585* (US). **San Martín**: Alto Río Huallaga, 360–900 m, Dec. 1929, *Williams 5800* (F, GH, NY, US).

Henrard (1941) menciona que *P. quadriglume* sería una especie teratológica, por el hecho de poseer 4 "glumas," de las cuales indica que la cuarta corresponde a una gluma III y no a la lemma de la segunda flor. Sin embargo el análisis de abundante material de la especie descarta la hipótesis de Henrard, coincidiendo así con lo anteriormente expuesto por Palacios (1968).

Esta peculiar estructura de la espiguilla es prácticamente unica dentro del material examinado hasta el momento, en el género *Panicum*, habiéndose hallado ocasionalmente una estructura similar en un especimen de *P. crateriferum* Sohns (Zuloaga & Sendulsky, 1988).

En esta especie se observa, tal como en *P. peladoense* y *P. exiguum*, que los antecios son negruzcos y caedizos independientemente de las glumas a la madurez de la espiguilla.

30. Panicum stramineum Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 67, fig. 50. 1910. *Panicum capillare* L. var. *stramineum* (Hitchc. & Chase) Gould, Madroño 10: 94. 1949. *Panicum hirticaule* J. Presl var. *stramineum* (Hitchc. & Chase) Beetle, Phytologia 47: 383. 1981. TIPO: México, Sonora: Guaymas, 1887, *Palmer 206*,** (holótipo, US-592753; isótipos, F, NY, SI, US-742139, 823636, 823638, W). Figura 28.

Panicum caatingense Renvoize, Kew Bull. 37: 325. 1982. TIPO: Brasil. Bahia: 41 km N of Senhor do Bonfim on the BA 130 highway to Juazeiro, 50 m, 26 Feb.

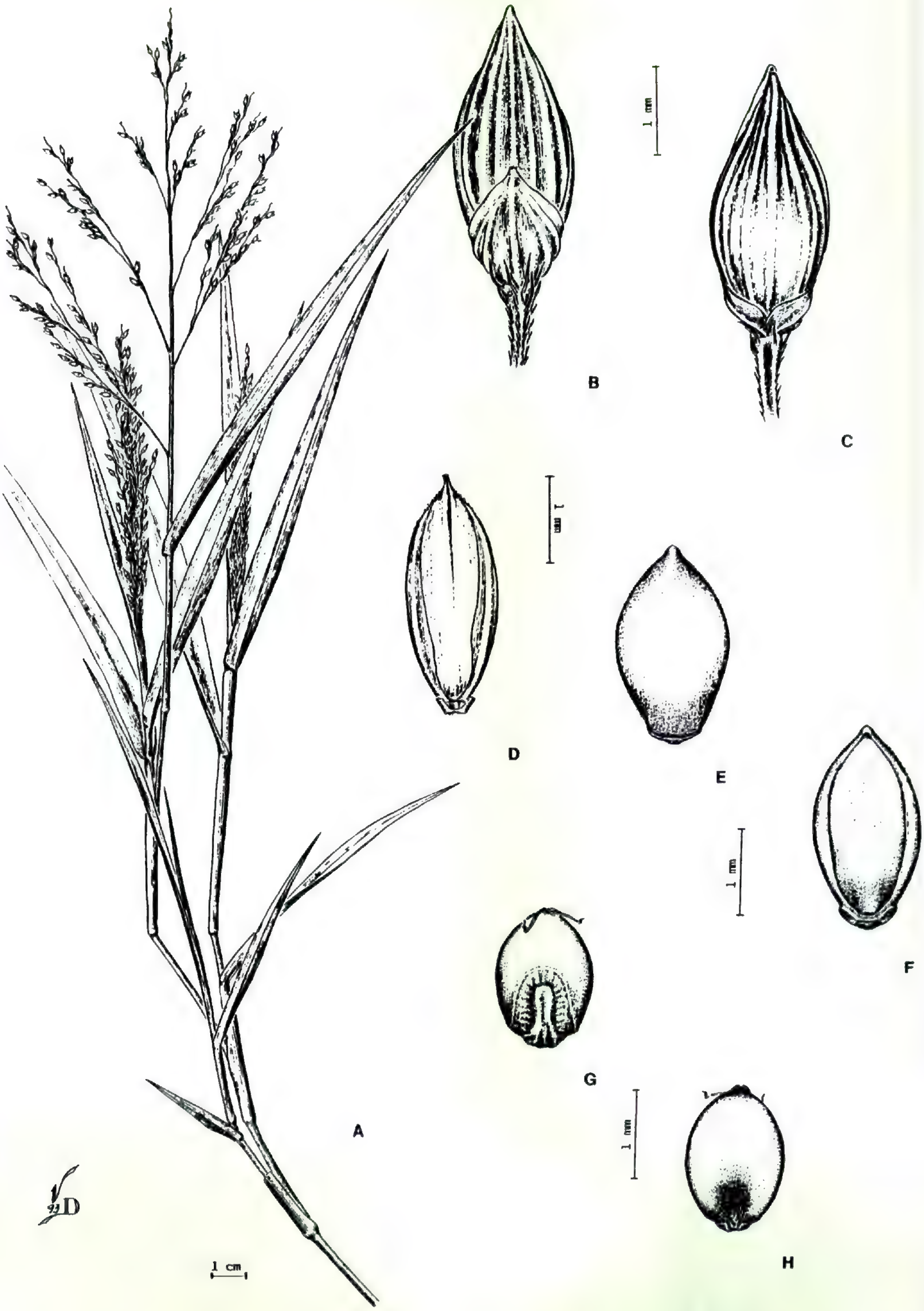


Figura 28. *Panicum stramineum.*—A. Porción de una caña florífera.—B. Espiguilla vista del lado de la gluma inferior.—C. Espiguilla vista del lado de la gluma superior.—D. Pálea inferior.—E. Antecio superior visto del lado de la lemma.—F. Antecio superior visto del lado de la pálea.—G. Cariopsis, vista escutelar.—H. Cariopsis, vista hilar. (*Palmer 206.*)

1974, *Harley et al. 16384* (holótipo, CEPEC; isótipos, K, RB, US-2955107).

Plantas anuales, cespitosas. *Cañas* erectas de 10–70(–125) cm de alto, geniculadas y ramificadas en los nudos inferiores; entrenudos de 2–15 cm de largo, cilíndricos, glabros; nudos corta a largamente pilosos. *Vainas* de 2–9 cm de largo, glabras a hirsutas, con pelos papilosos, verdes a purpúreas, con los márgenes membranáceos, glabros, o con un margen pestañoso. *Lígulas* membranáceo-pestañosas, de 0.9–2.4 mm de largo, con largos pelos por detrás en la base de la lámina o sin los mismos; cuello glabro a híspido. *Láminas* linear-lanceoladas, de 4.5–30(–42) cm de largo, 0.3–1.3(–2) cm de ancho, las basales de menor tamaño, erectas, ascendentes, poco divergentes, planas, glabras a esparcidamente papiloso-pilosas en ambas caras, de base redondeada y ápice atenuado, con los bordes escabriúsculos, glabros a papiloso-pestañosos hacia la base. *Pedúnculos* hasta de 24 cm de largo, cilíndricos, glabros. *Inflorescencias* terminales exertas, laxas, de 2.5–22(–38) cm de largo, (1–)4–10(–20) cm de ancho; *eje principal* anguloso, escabriúsculo; pulvínulos glabros a cortamente pilosos; ramificaciones de primer orden alternas a subopuestas, divergentes, desnudas hacia la base; ramificaciones de segundo orden escabriúsculas, divergentes, con espiguillas dispersas sobre los ejes; pedicelos claviformes de 0.7–2.5 mm de largo, escabriúsculos, con pelos blanquecinos hacia el ápice. *Inflorescencias axilares* presentes, similares a las terminales. *Espiguillas* globosas, de 2.3–3.2 mm de largo, 0.8–1.4 mm de ancho, túrgidas, abruptamente acuminadas, no estipitadas, pajizas; gluma superior y lemma inferior subiguales, tan largas como el antecio superior o superándolo 0.4 mm. *Gluma inferior* ovado-acuminada, de 0.7–1.2(–1.5) mm de largo, ⅓–½ o un poco más del largo de la espiguilla, de ápice obtuso a agudo, 5–7-nervia, el nervio medio escabriúsculo hacia el ápice. *Gluma superior* de 1.8–3.1 mm de largo, 9–11(–13)-nervia. *Lemma inferior* glumiforme, 1.7–3 mm de largo, 9–11-nervia. *Pálea inferior* ovado-lanceolada, de (1.4–)2.3–2.7 mm de largo, 0.5–0.9 mm de ancho, igual o más larga que el antecio superior, membranácea, hialina, glabra, con los márgenes superiores ciliados a glabros. *Antecio superior* elipsoide, de 1.5–2.5 mm de largo, 0.7–1.3 mm de ancho, crustáceo, liso, lustroso, pajizo y con tintes grisáceos a la madurez, con dos cicatrices basales de 0.2 mm de largo; lemma 7-nervia; pálea con papilas simples hacia el ápice, en ocasiones distribuidas en toda la superficie. *Cariopsis* ovoide, de 1.2–1.6 mm de largo, 0.6–0.9 mm de ancho, pajiza; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Presente en los Estados Unidos de América y México y en América del Sur desde Venezuela hasta la Argentina (Fig. 9). Crece en campos o en sitios abiertos en bordes de caminos o vías férreas. Es también frecuente en bosques decíduos o en sitios inundados, ocasionalmente apoyante sobre la vegetación; habita desde el nivel del mar hasta 1100 m de elevación.

Nombre vulgar. "Capim-lanudo" (en Brasil).

Material representativo citado. ARGENTINA. **Catamarca**: Santa Lucía, 2 abr. 1950, *Brizuela 982* (GH, NY). **Formosa**: Dpto. Matacos, Ingeniero Juárez, 14 ene. 1957, *Burkart 20275** (SI, US). **Jujuy**: Dpto. San Pedro, Chaguaral, Finca Jure, 18 abr. 1983, *Ahumada & Castellón 4829*** (SI). **La Rioja**: Dpto. Gral. San Martín, Estancia La Diana, ca. 800 m, Mar. 1907, *Kneucker 730* (GH, ISC, LA, MO, NY, SI, W). **Salta**: Dpto. Campo Santo, Güemes, 3 abr. 1945, *O'Donell 2629* (NY, SI). BOLIVIA. **Beni**: Trinidad, 9 abr. 1979, *Krapovickas & Schinini** (SI); Prov. Gral. Ballivian, Espíritu, en la zona de influencia del río Yacuma, 200 m, 12 mar. 1990, *Beck 15176* (SI). **Chuquisaca**: Isirenda, 26 ene. 1992, *Saravia Toledo & Nelson Joaquin 10412* (SI). **Santa Cruz**: Chiquitos, Est. San Ignacio, 22 km N of San José de Chiquitos, 17°35′S, 60°45′W, 320 m, 1 Feb. 1986, *Killeen 1711* (F, SI). BRASIL. **Bahia**: 4 km north of Senhor de Bonfim, disturbed ground by roadside, 550 m, 40°11′W, 10°27′S, 24 Feb. 1974, *Harley et al. 16294* (MO, R, RB, US). **Ceará**: Iguatú, *Swallen 4396* (GH, RB, US). **Maranhao**: Mun. Loreto, Ilha de Balsas, region between the Balsas and Parnaiba rivers, 26 km south of Loreto, 200 m, 11 Feb. 1970, *Eiten & Eiten 10579* (US). **Mato Grosso do Sul**: Base do Cerro do Urucum, 23 km S Corumbá, 22 nov. 1977, *Allem & Vieira 1479** (MO, SI). **Piaui**: Fazenda Nacional to Picos, low ground near small stream, 4 abr. 1934, *Swallen 4192* (RB, US). **Para**: Ilha do Marajó, Faz. Gavinho, *Goeldi 261* (NY). ESTADOS UNIDOS DE AMERICA. **Arizona**: Pima Co., 18 Aug. 1937, *Proctor 2571* (US); under Mezquite bushes, White's Mills, 5 Sep. 1867, *Palmer 270* (MO). MEXICO. **Chiapas**: Mun. Arriaga, deciduous forest, at Río Las Arenas, 15 km northwest of Arriaga, 130 m, 27 Aug. 1974, *Breedlove 36779-A* (MO). **Guerrero**: Lagunillas, 1 Aug. 1898, *Langlassé 263* (US). **Michoacán**: Tancitaro, road to Hda. California, 1000 ft., 12 Aug. 1941, *Leavenworth & Hoogstraal 1453* (GH, MO, NY, US). **Nayarit**: entre Concepción y Acaponeta, 29 jul. 1897, *Rose 1889** (MEXU, NY, US); entre Rosario y Acoponeta, 28 jul. 1897, *Rose 1883* (US); 26.8 mi. S of Sinaloa state line in Nayarit, 24 July 1975, *Dunn et al. 21855** (MO, NY). **Nuevo León**: 12 mi. S of Monterrey, 14 July 1933, *Mueller 404* (US). **Oaxaca**: Ixtepec, Aug. 1935, *Fisher 35314** (F, MO, NY, US); along the Hwy. to Ixtepec, 1 km NW of Juchitán, 100 m, 26 July 1958, *King 771* (MEXU, US). **Sinaloa**: entre Rosario y Acaponeta, *Rose 1878* (GH, US); vicinity of Labradas, 18 Sep. 1925, *Ferris & Mexía 5069* (MO, US). **Sonora**: Orozi, near Río Yaqui, 7 Sep. 1935, *Pennell 20221* (MO, US). PARAGUAY. **Alto Paraguay**: Colonia San Lázaro, cerca del Río Apa, ene. 1931, *Rojas 5476a* (US). **Boquerón**: Tinpunké, cercanía Río Pilcomayo, 28 oct. 1985, *Mereles 715* (SI); entre las Estancias Santa Ramona y San Alberto, Puesto Sastre, 9 mar. 1949, *Ramírez 51* (SI). **Nueva Asunción**: Parque Nacional Tte. Enciso, 21°10′S, 61°35′W, 10 ene. 1984, *Hahn 1911* (MO, SI). **Presidente Hayes**: Ruta Concepción–

Pozo Colorado, a 28 km del puente, 18 feb. 1990, *Palacios 1856* (MO). **Sin Departamento**: San Salvador, 4 mar. 1917, *Rojas 11027* (US). PERU. **Tumbes**: along the road to Tutumo, about 20 km from Tumbes, 26 abr. 1969, *Simpson & Schunke V. 829** (F, US). VENEZUELA. **Apure**: entre los caños Balza y Manati, carretera Mantecal-Quintero, 7°45′N, 69°40′W, 5 ago. 1989, *Zuloaga et al. 4340** (MO, SI, VEN); entre Achaguas y San Fernando, cerca de Bethel, 7°48′N, 67°55′W, 6 ago. 1989, *Zuloaga et al. 4350** (SI); Mantecal, 17 jul. 1975, *Ramia & Montes 5345** (US, VEN). **Carabobo**: Valencia, aprox. 4 km al E de Valencia en la autopista entre Valencia y Maracay, 8 jun. 1978, *Burandt Jr. & Wingfield V0242* (VEN). **Falcón**: Paraguaná, 2 km E de Sta. Ana, 4 ene. 1980, *Wingfield 7361* (VEN). **Guárico**: S de Calabozo, 22 jul. 1976, *Castillo 583** (VEN). **Zulia**: Perijá, carretera Las Piedras-San José-Las Laras, en Km 9 al E del empalme con carretera Perijá, 10 sep. 1977, *Bunting 5447* (VEN). **Sin Estado**: Hato Becerra, a 2 km S del Río Orituco, 11 jul. 1961, *Blydenstein 148* (VEN).

Zuloaga (1987a) sinonimiza esta especie con *P. hirticaule* y posteriormente Zuloaga (1989) y Killeen (1990) citan material de Sudamérica austral de *P. stramineum* bajo *P. hirticaule*. Recientemente Davidse (1994) correctamente revalida la especie, señalando, entre los caracteres distintivos de la misma, que posee espiguillas más obtusas y divergentes con gluma inferior relativamente más pequeña y pálea inferior mucho más larga. *Panicum caatingense*, especie sinonimizada con *P. hirticaule* por Zuloaga (1989) y Killeen (1990) debe ser considerada en la sinonimia de *P. stramineum*.

En *P. stramineum* la gluma inferior varía entre ⅓ y ½ del largo de la gluma superior y la lemma inferior.

Esta especie es afín a *P. hirticaule*, de la que se diferencia por poseer espiguillas globosas, túrgidas, más o menos abruptamente acuminadas y con la pálea inferior desarrollada, alcanzando el mismo largo de la lemma inferior. Las plantas usualmente tienen láminas erectas, poco divergentes del caule.

El ejemplar *Simpson 829*, de Perú, tiene espiguillas similares a *P. stramineum*, pero la gluma inferior es un poco mas larga que ½ y los pedicelos son aparentemente glabros y los ejes esparcidamenten pilosos.

31. Panicum tamaulipense F. R. Waller & Morden, Syst. Bot. 8: 221. 1983. TIPO: México. Tamaulipas: Sierra de Tamaulipas area, between La Chona and Río Santa Olaya, low deciduous forest, 50 m, 26 Sep. 1956, *Martínez Martínez & Borja Luyando F-2161* (holótipo, TEX no visto; isótipo, US-2463101).

Plantas perennes, cespitosas, de 50–80(–120) cm de alto. *Cañas* simples, glaucas, innovaciones intravaginales, erectas, paucinodes; entrenudos de 3–10 cm de largo, cilíndricos, huecos, de 1–2 mm diám. en su base; nudos pilosos con pelos cortos. *Vainas* de 8–12 cm de largo, iguales o mayores que los entrenudos, estriadas, hirsutas, con tintes violáceos, con pelos tuberculados adpresos, un margen pestañoso, el restante glabro. *Lígulas* membranáceo-ciliadas de 0.5–1.2 mm de largo; cuello piloso a glabro. *Láminas* linear-lanceoladas, de 20–35(–50) cm de largo, 0.5–0.8 cm de ancho, erectas, ascendentes, rígidas, planas, ligeramente rizadas en la base, glaucas, glabras, de base angostada y ápice agudo, con los bordes ligeramente involutos, escabriúsculos, el nervio medio manifiesto. *Pedúnculos* hasta de 50 cm de largo, glabros, lisos, pajizos o con tintes violáceos. *Inflorescencias* exertas, de 15–30 cm de largo, 6–15 cm de ancho, ramificaciones inferiores hasta de 18 cm de largo; *eje principal* escabroso, glabro, ligeramente ondulado; pulvínulos glabros, ramificaciones de primer orden alternas, divergentes, pedicelos claviformes, de 4–15 mm de largo, divergentes, flexuosos, glabros, escabriúsculos. *Espiguillas* ovoides, de 1.8–2.2 mm de largo, 0.7–1 mm de ancho, de ápice abruptamente acuminado, no estipitadas, glabras, pálidas o con tintes violáceos hacia el ápice, con los nervios verdosos; gluma superior y lemma inferior subiguales, tan largas como el antecio superior. *Gluma inferior* ovado-acuminada, de 1–1.2 mm de largo, alcanzando ½ del largo de la espiguilla, 5-nervia. *Gluma superior* de 1.8–1.9 mm de largo, acuminada, 7–13-nervia. *Lemma inferior* glumiforme, de 1.8 mm de largo, 7–9-nervia. *Pálea inferior* lanceolada, de 1–1.2 mm de largo, 0.3 mm de ancho, ¾ del largo del antecio superior, membranácea, hialina, glabra, de ápice finamente denticulado. *Antecio superior* ovoide, de 1.5–2 mm de largo, 0.6–1 mm de ancho, crustáceo, glabro, liso, lustroso, con dos cicatrices basales ca. 0.2 mm de largo, castañas a la madurez; lemma 7-nervia, pálea papilosa hacia el ápice. *Cariopsis* ovoide, de 1 mm de largo, 0.5 mm de ancho, blanquecina; hilo punctiforme; embrión ½ del largo de la cariopsis.

Distribución y ecología. Endémica de México, donde se encuentra en campos de los departamentos de San Luis Potosí y Tamaulipas (Fig. 9); llega hasta los 350 m; florece y fructifica entre mayo y diciembre.

Material adicional examinado. MEXICO. **San Luis Potosí**: El Banito, 100 ft, 22 July 1939, *Chase 7558* (US); Mun. El Pujal, *Chase 7492* (US); 2 miles S of Huichihoayan, *McGregor et al. 870** (US); Ciudad Valles, 5 May 1962, *Beetle M-718* (US); Valles, 800 ft., 17 July 1933, *Fisher 3313* (US); in a tropical forest along Mexico Highway 55 to Xilitla, *Sohns 1431* (US). **Tamaulipas**: El Mante to Limón, 3 May 1931, *Swallen 1618* (US); 64 km from Soto La Marina on the road to Casas and Victoria, 350 m,

4 Oct. 1956, *Martínez Martínez & Borja Luyando F-2364* (US); 35 km from Victoria on the road to Casas and Soto La Marina, 280 m, 3 Oct. 1956, *Martínez Martínez & Borja Luyando F-2333** (US); 5 mi. N of San Rafael toward Soto la Marina, 800 ft., 11 Dec. 1959, *Crutchfield & Johnston 4956* (MEXU).

Especie afín a *P. hallii* var. *filipes*, de la que se distingue por tener espiguillas menores, de 1.8–2.2 mm de largo y láminas de 20–35(–50) cm de largo por 0.5–0.8 cm de ancho.

Taxon Dudoso

Panicum capillare var. *minus* Döll, in Martius, Fl. Bras. 2(2): 202. 1877.

Doell indica que esta variedad posee panoja pauciflora y hace referencia a la cita de Nees de *Panicum philadelphicum* (en la que este autor incluye a *P. capillare* var. *minus* Muhl. en la sinonimia de *P. philadelphicum*).

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Apendice. Cada especimen es citado por el primer nombre del colector en el caso en que otros coleccionistas participen de la colección. Se indica entre paréntesis el número de la especie: *Panicum alatum* var. *alatum* (1a), *P. alatum* var. *longiflorum* (1b), *P. alatum* var. *minus* (1c), *P. aquarum* (2), *P. aztecanum* (3), *P. bergii* var. *bergii* (4a), *P. bergii* var. *pilosissimum* (4b), *P. capillare* (5), *P. capillarioides* (6), *P. chasei* (7), *P. decolorans* (8), *P. diffusum* (9), *P. ephemeroides* (10), *P. exiguum* (11), *P. flexile* (12), *P. furvum* (13), *P. ghiesbreghtii* (14), *P. hallii* var. *hallii* (15a), *P. hallii* var. *filipes* (15b), *P. hillmanii* (16), *P. hirsutum* (17), *P. hirticaule* var. *hirticaule* (18a), *P. hirticaule* var. *verrucosum* (18b), *P. hispidifolium* (19), *P. lepidulum* (20), *P. magnispicula* (21), *P. miliaceum* (22), *P. mohavense* (23), *P. mucronulatum* (24), *P. pampinosum* (25), *P. parcum* (26), *P. peladoense* (27), *P. philadelphicum* (28), *P. quadriglume* (29), *P. stramineum* (30) y *P. tamaulipense* (31).

Abbott 1027 (9); *Abrams 12902* (30); *Agniel 10269** (8), *10393* (8); *Ahart 6168* (22); *Ahumada 911* (4a), *1502* (4a), *4829*** (30), *5023* (30); *Ainslie s.n.* (12); *Alberdi 12269* (22); *Allard 10422* (12), *14148* (14), *15744* (9) *15902* (9); *Allem 1479* (30), *2145* (30), *2233* (11); *Alston 5235* (14), *5298* (14); *Alvarez 603* (4a); *Amer. Gr. Hb. 504* (15a); *Anderson 358* (12), *897*, *899* (18a), *1365* (19), *2096* (5), *7381** (11), *s.n.* (1c); *Andrade Lima 71-6363* (11); *Araujo 151* (7), *186* (7), *289* (4a), *527* (7); *Archer 3400* (8), *3968* (14); *Arechavaleta 24a* (4a); *Aristeguieta 4301* (19), *4334* (19), *5665* (19), *5755* (19); *Arsène 2417** (20), *2864* (20), *2985* (20); *Artupo R. 1723* (15a); *Arzivenco 640* (5), *950* (27); *Aviña 1248* (18b).

Badillo 7 (14), *146* (14), *690* (14); *Báez s.n.* (22); *Bain s.n.* (28); *Balansa 12* (4a), *13* (27), *14* (27), *15* (4a), *4357*** (27); *Baldwin Jr. 14321** (8); *Balick 133* (11); *Ball 20* (5), *120* (5); *Bang 493** (29); *Barkley 701* (8), *7639* (8); *Barkworth 5113* (15a); *Barneby 2455* (15a); *Barreto s.n.* (7); *Bartlett 1024* (28), *10549* (15a), *10591* (15a), *21345* (4a); *Basile 51* (8), *52* (8); *Bebb 5796* (28), *5957a* (12); *Beck 761* (11), *9921* (4a), *15176* (30); *Beetle 1031* (15b), *1061* (15a), *1077* (15a), *1772* (4a); *Beetle M-718* (31), *M-917* (14), *M-1211* (1a), *M-2551* (18a), *M-2646* (18a), *M-7030* (18a), *M-7324* (20); *Benedict Jr. 2963-A* (28); *Bennett s.n.* (12); *Bernal s.n.* (15a); *Bertero s.n.* (17); *Bertero s.n.* (9); *Bertoni 5381* (4a), *5532* (27), *5534* (27); *Black 86C* (11), *88C* (11), *51-11086* (29), *51-11413* (4a), *51-11686* (29), *54-16594* (30); *Blair 731* (11); *Blake 7326A* (18a); *Blanchard s.n.* (5); *Blanchet 2961* (24); *Blanco 512* (1c); *Blankinship s.n.* (16); *Blumer 1683* (15a);

Blydenstein 148 (30), *1846* (2); *Boege 1858* (18a); *Boelcke 11889* (4a); *Boom 6189* (19); *Bourgeau 2751* (14); *Box 18* (14), *39* (14), *49* (14), *176* (17), *190* (17), *3703* (17), *3836* (17); *Brace 4812* (14); *Brade 8144* (27); *Brandegee 4* (26), *8* (1a), *42* (1c); *Braum 2648* (12), *2687* (12), *s.n.* (12), *s.n.* (5); *Breedlove 10630* (1c), *13492* (26), *13833* (26), *27334* (18a), *28359* (26), *28837* (17), *36779-A* (30), *36852* (20), *36875* (26), *37573* (19), *37654* (19), *41540* (18a), *46945* (17), *51680* (18a), *52871* (26), *54261* (26), *54117* (26), *54908* (14), *55245* (17), *56081* (18a); *Britton 314* (9), *382* (9), *424* (9), *649* (9), *745* (14), *1380* (9), *2356* (9), *4064** (9), *6123* (9), *6349* (14), *6859* (9), *13177* (9); *Brizuela 982* (30); *Broadway 2629* (17), *4586* (17), *4895* (17), *9291* (17); *Brown 21* (5), *569*,*** (28); *Brunken 241* (15a), *360* (26), *368* (26), *434* (8), *444* (20); *Buchtien 4174* (29); *Bunting 5447* (30), *5568* (30), *5663* (30), *Burandt Jr. V0238* (17), *V0242* (30), *V0498* (11); *Burchell 6769* (29), *6794-2* (27), *6827* (11), *8813* (2); *Burger 7875* (19); *Burkart 997* (7), *1080* (7), *12262* (30), *13325* (22), *14367* (3b), *14455* (4a), *14616* (4a), *15677* (4a), *15943* (5), *16447** (17), *16508* (14), *16870* (14), *17012* (14), *17190* (19), *17204* (18a), *17262* (19), *17732* (4a), *17743* (4a), *18397* (4a), *18643* (4a), *19692* (4a), *20264* (5), *20275** (30), *22122* (4a), *23269* (5), *24109* (22); *Bush 722* (28), *858* (15a), *1087* (12), *1156* (15a), *5120* (28), *s.n.* (28).

Cabanillas 15 (18a), *17* (18a); *Cabrera 772* (4a), *2237* (17), *2461* (17), *2484* (4a), *2630* (17), *7008* (4a), *9837* (4a), *11739* (14), *22167* (27), *25988* (4a), *2652* (30), *28697* (4a), *29057* (4a), *32328* (4a), *32385* (27), *32388** (27), *32416* (4a), *32423*,*** (7), *32704* (4a), *34220* (30); *Calderon 1672* (22); *Calzada 4492* (17), *6250* (17); *Camby 6* (1b); *Campelo 2154* (24); *Canby 221* (12); *Canoniero 92* (3b); *Cárdenas 1647* (30), *3533* (30), *3534* (30); *Carter 5* (1c), *4726* (1a), *4788b* (1c), *4970*,*** (1b), *5016* (18a), *5074*** (1b), *5353* (1b), *5374* (1b), *5548* (1b); *Casali 44* (4a), *47* (4a); *Casco 46* (18a); *Castaneda 8948* (17); *Castellanos 43** (27), *25909* (30), *s.n.* (4a); *Castillo 583** (30), *s.n.* (5); *Castro 69* (18a); *Catalán 92* (26); *Chase 1473* (12), *1474* (12), *1479* (12), *2726* (5), *4986* (5), *5900* (15a), *6308* (9), *6547* (14), *6567* (9), *6577* (9), *6744* (14), *6856* (28), *7089* (20), *7090** (8), *7256* (15a), *7270** (8), *7480* (14), *7492* (31), *7558** (15b), *8105** (24), *8105bis* (24), *8696* (27), *88021/2* (29), *8897*,*** (29), *9089* (9), *9279* (27), *9300** (11), *10151* (4a), *10450* (29), *10534* (27), *10589* (27), *10665* (27), *10697* (27), *10723* (27), *10725* (11), *10780** (27), *10786* (27), *10846* (11), *10866* (29), *10886** (27), *10976** (29), *11049* (29), *11071** (27), *11119* (11), *11207* (27), *11280* (27), *11465* (11), *11482* (11), *11560** (29), *11638* (11), *11641* (11), *11791** (11), *11858* (27), *11924* (29), *11990* (29), *12115* (29), *12389* (11), *12607* (14), *s.n.* (28), *s.n.* (5), *s.n. Amer. Gr. Nat. Herb. #22* (28); *Chavelas ES-109* (14); *Chiang 191* (14), *294* (15a), *9201* (15a), *12097* (15a); *Christ 19* (12); *Christian s.n.* (22); *Churchill 7* (22), *103* (28), *s.n.* (12); *Clayton 4366* (27), *4507* (27); *Coelho de Moraes 677** (24); *Collins 151* (5); *Colunga 44*** (18b); *Conzatti 3603* (20); *Cook 78* (9); *Coradin 3394* (24); *Cordini 20* (7); *Correll 17122* (15a), *17274* (15b); *Cory 28458* (6); *Cowan 3398* (18a); *Crespo s.n.* (22), *17* (14), *70* (14); *Cristoff 181* (18a); *Croat 23483* (17), *23664* (17), *47699* (18a); *Croft 240* (6); *Crowe 545B* (17); *Crutchfield 4956* (31), *6068* (15b); *Curran 250* (17), *261* (17); *Curtiss 384* (9), *494** (9), *6867* (22); *Cutler 9084* (29).

D'Arcy 3830 (12); *Da Silva 1* (11), *7* (11), *124* (11), *137* (11), *144* (29); *Dalby 44* (4a); *Darrow 3419* (15a); *Davidse 2510* (17), *2925* (19), *2950* (19), *4314* (19), *9492* (14), *9550* (26), *9587* (26), *9657* (20), *9806* (20), *9912** (20), *9927** (20), *10057* (15a), *10618* (27), *10712* (27), *11145* (27), *18161* (4a), *18851* (17), *20246* (17), *20271* (17), *20528* (17), *20612* (17), *29687* (26), *31533** (19), *31553* (19), *31651* (1c), *31665** (18a), *31704* (1c), *32004* (17), *32401* (17), *32638** (14); *Davis 61068* (24), *s.n.* (17), *s.n.* (28); *Dawson 400* (4a), *424* (4a), *713* (22), *P1702* (22), *3355* (22); *de Granville 9138* (22); *de la Sagra 10* (17); *de la Sota 4257* (4a); *de Wet 4343* (30), *4354** (1a), *4732* (1a); *Deann 42277** (12); *Del Puerto 685* (4a), *1527* (27); *Delascio 11585* (19); *Demaree 27528* (28), *30200* (12), *33174* (5), *64207* (28); *Díaz Luna 2044* (1c); *Dodge 1* (12), *7* (12), *124* (12), *5610* (17), *s.n.* (12); *Dodson 12506* (18a), *12514* (18a); *Dombrowski 11096* (27); *Dorantes 246bis* (18a), *1152* (14), *1510* (1c); *Dore 46-137* (5), *10544* (5), *12887* (5), *s.n.* (5); *Drouet 1953* (27), *Ducan 100* (16), *1438* (28), *4172* (28); *Dueñas 2* (19); *Duke 303* (17), *10142* (17), *14117* (17); *Duncan 13221* (12); *Dunn 21855** (30); *Duss 12* (14), *536* (9), *668* (14), *676* (9), *768* (17), *3181** (9), *3184* (14), *3917* (17), *s.n.** (14); *Dwyer 2781* (18a).

*Earle 302** (15a); *Eggers 76*** (9), *5315* (14), *5406* (14), *14538* (17), *14949* (14), *15419** (14); *Eggert 58* (28), *s.n.* (12), *s.n.* (16), *s.n.* (28); *Eggleston 22396* (12); *Eiten 2116* (27), *3956* (11), *4504* (11), *10579* (30); *Ekman H20* (9), *755* (17), *995* (9), *1200* (9), *1442* (14), *1517* (9), *1987* (14), *2011* (14), *2151* (9), *3419* (17), *4392* (17), *5791* (17), *6118* (17), *6183* (17), *7483* (9), *7511* (9), *8534* (17), *9667* (14), *9991* (18a), *10068* (?), *11732* (9), *12036* (14), *12686* (14), *13275* (17), *13390* (9), *16129* (14), *16237* (9), *16312* (17), *17578* (17); *Enriquez 347* (17); *Eskuche 2538-5** (27); *Evans s.n.* (18a); *Ezcurra s.n.* (1c).

Fabris 1080 (5); *Farwell 893* (12); *Fassett 25492* (14); *Felger 86-339* (1c); *Felippone s.n.* (5); *Fendler 2565* (11); *Fernald 519* (5), *9259* (28), *19754* (5), *41415* (12); *17828* (5); *Ferreyra 5929* (18a); *Ferris 3175* (17), *5069* (30), *5070* (1c); *Fueillet 4442* (22); *Fiebrig 112* (29), *5095* (29), *5102* (29); *Filgueiras 1060** (27), *1204* (22), *1332* (11), *2282* (11); *Fisher 3313* (31), *35314** (30); *Fishlock 206* (14); *Flores 1053* (26), *1197* (26); *Fontana F57-7* (27), *F94-56* (27); *Fortuna 2* (4a), *s.n.* (5); *Fosberg 27768* (29); *Fournier 283* (1c); *Fowler 8d* (18a); *Freeman 53433*** (28).

Gail s.n. (5); *Galli 172* (4a); *Gallinal PE-1290* (4a), *PE-2362* (4a), *PE-4473* (7); *Gándara 2* (18a); *Garaventa 2847* (5); *Gardner 1838* (24); *Garnier 833* (18a); *Garófalo 163** (19), *381* (4a); *Gaumer 1501* (18a), *2477* (14); *Gehrt 31509* (22); *Gemtchujnicov 369* (2), *s.n.** (27); *Gentle* 7120 (17), *8380* (17); *Gentry 1841* (18a), *6667* (26), *8349* (15a), *14353*,*** (1a); *Gereau 1044* (12), *2230* (18a); *Giardelli 256* (4a), *616* (22); *Gilly 243* (17); *Gilman 37* (18b); *Glassman 2145* (19); *Glaziou 13338* (4a); *Goeldi 111* (17), *128* (17), *261* (30); *Gómez 8243* (30), *824* (30); *Gonçalves s.n.* (11); *González Medrano 14252* (15a); *González s.n.* (20); *Goodding 192–45* (30), *243* (5), *418* (18a), *4030* (15a); *Gouin 6* (17), *21* (14); *Gould 1187* (15a), *2409* (15a), *3192* (18a), *3748* (18a), *4468* (18a), *4510* (18a), *4550* (18a), *4937* (15a), *5086* (18a), *7579* (15a), *7674* (15a), *7685* (15b), *7707* (15a), *7906* (15a), *9244* (18a), *9558* (1c), *9643* (20), *9763* (15b), *10292* (15b), *10796* (20), *10929* (15a), *10956* (15b), *10972* (15b), *10973* (15b), *11000* (6), *11075a* (15a), *11157* (15a), *11271* (15b), *11282* (15a), *11302* (15a), *11456* (6), *11557a* (15a), *11596** (8), *11669* (26), *11676* (26), *11796* (15a), *12032* (18a), *12071* (1a), *12084* (1c), *12110** (1a), *12171* (18a), *12288* (26), *12322* (20), *12729** (26), *12757* (26); *Greene 258* (1c), *13107*

(1c); *Greenman 5047* (12), *5101* (12); *Griffiths 28* (18a), *238* (15a), *399* (5), *684* (5), *5004* (15a), *6939 1/2* (18b), *6939 1/2* (25), *7194* (18b), *7317* (1a), *7808* (15a); *Grijalva 4016* (18a); *Grinnell 1082a* (1c); *Grisol 36* (30); *Guaglianone 270* (4a), *360* (4a), *473* (4a), *595* (4a), *667* (4a); *Guardado s.n.* (20); *Gutzar 1850* (26); *Gunther 5* (5).

*Haenke s.n.*** (18a); *Hage 1716* (24); *Hahn 1232* (9), *1911* (30); *Hall 816*** (15a), *9813* (15a); *Halley 69* (6); *Hamilton 230* (14); *Hammel 11795* (17); *Hanes s.n.* (12); *Harley 16294* (30); *Harper 184* (28), *3759** (12); *Harriman 15627* (14); *Harrington 3361* (15a); *Harris 40** (19), *197* (19), *11691* (14), *12161* (14), *12164** (9); *Harvey 950* (15b), *1186** (15b), *1378* (18a), *1516* (15a), *1578** (8), *1600* (18a), *1653* (18a), *6667* (26); *Hassler 1942* (9), *10967* (29), *10986* (11), *11682* (29), *12099* (27), *12494* (29), *13022* (29); *Hatch 4615* (6), *5054* (15a); *Hatschbach 23576* (29), *43533* (27), *46144* (29); *Hayden 8220* (5); *Heller 701* (12), *13864* (5), *s.n.* (28); *Henderson 68-852* (12); *Henrich 139* (18a); *Hermann 6996* (12); *Hernández 240** (18b), *N-1667* (20), *N-1911* (15a); *Hernández Xolocotzi X-2304* (8), *2468* (26), *X-2775* (18a), *X-2791* (1c), *2793* (8), *X-3379* (17); *Herrera Castro 84* (18b); *Hers 4000* (30); *Herter 544* (4a), *s.n.* (4a); *Hess 1459* (14); *Hicken 22* (4a); *Hicks 813*(12); *Higgins 6990* (30); *Hill s.n.* (12); *Hinton 166* (18a), *1062* (18a), *1424* (14), *1428* (14), *1996* (26), *2000* (26), *2010** (3), *4413* (14), *4442* (18a), *6337* (18a), *6423* (1a), *6686* (26), *9284* (18a); *Hitchcock 7* (128), *165* (28), *220* (15b), *2798* (5), *3481* (18a), *3494* (1c), *3526* (18b), *3541* (1c), *3547* (1c), *3553* (1a), *3573* (1c), *3604* (18a), *3631* (18a), *3675* (1c), *3706* (15a), *5143* (15b), *5197* (5), *5293* (15a), *5318* (15b), *5349* (6), *5385* (15b), *5395* (15b), *5537* (15a), *5547** (6), *5605* (15a), *5712** (8), *5719 1/2* (15a), *5756* (20), *5822* (8), *5864* (8), *5958* (20), *6057* (8), *6063* (20), *6143* (14), *6363* (14), *6391* (14), *6418* (14), *6782* (26), *6808* (26), *6810* (26), *6811* (26), *6814* (18a), *7031* (17), *7081* (26), *7089** (18a), *7117* (20), *7199* (20), *7238* (20), *7424* (18a), *7510* (20), *7591* (20), *7751* (25), *7957* (17), *7964* (17), *7997* (14), *8014* (14), *8065* (14), *8094* (14), *8382* (17), *8397* (17), *8435* (17), *8452* (14), *8517* (18a), *8601* (14), *8687** (14), *8755* (14), *8794* (1c), *8924* (18a), *8993* (14), *9014* (20), *9463* (9), *9927* (19), *13255* (15a), *13333* (1c), *13411* (15a), *13445* (15a), *13490* (15a), *13517* (15a), *13539* (15a), *13597* (15a), *16121* (28), *16219* (15a), *16382* (14), *20580* (17), *20601* (17), *22115** (11), *23239* (9), *23292* (14), *23396* (17), *23397* (14), *23470* (5), *35411/2* (1b), *s.n. Amer. Gr. Natl. Herb 21* (12), *s.n.* (15a), *s.n.* (16), *s.n. Amer. Gr. Hb. 36* (14), *s.n. Amer. Gr. Nat. Herb. 28* (18a), *s.n. Amer. Gr. Herb. 33* (15b), *s.n. Amer. Gr. Nat. Herb. 29* (8), *s.n. Amer. Gr. Nat. Herb. 32* (6), *s.n., Amer. Gr. Hb. 28* (1c); *Holm 286* (18a); *Hosseus 43* (4a); *Howard 8357* (17); *Howell 8728* (1C), *8590* (1c), *8827* (1c), *9076* (1c), *9965* (1c), *9757* (1c); *Humboldt s.n.*** (8); *Hunter 63* (14); *Hunziker 12* (5); *Hutchings s.n.* (15a); *Hyacinth 960* (28).

Ibarrola 2533 (4a), *2611* (4a), *2889* (27), *3481* (27); *Iltis et al. 114* (15a); *Irwin 24519* (11); *Isely 15* (5), *4431* (28), *4596* (12).

Jack 6295 (17); *Jahn 197* (4a); *Janzen s.n.* (18a); *Jiménéz 530**** (14), *730* (14), *880* (14), *3620* (9), *4309* (17); *Johnston 467* (15a), *694* (15a), *1017** (15a), *1111** (15a), *4870* (15b), *7170** (15a), *7866* (18a), *7992**,** (1c), *8175* (15a), *8250* (15a), *8250a* (15a), *9104** (20), *10383* (15a), *11871* (15a), *12292* (18a); *Jones 24493* (1a), *s.n.* (18a), *s.n.* (1c).

Kappel s.n. (7); *Kay 9180* (16); *Kearney 72* (12), *151* (28), *960* (12), *961* (28), *12868* (5); *Kearney Jr. s.n.* (5); *Kellog s.n.* (22); *Killeen 823* (11), *856* (29), *891* (29), *1563* (29), *1702* (30), *1711* (30), *1770* (29), *1828* (29), *1848* (29), *2397* (29), *2834* (11); *Killip 4100* (14), *4326* (18a), *12174* (17), *37046* (4a); *King 771* (30), *919* (30), *3791* (14), *4679* (1c), *4831* (26); *Kneucker 730* (30); *Kral 33114* (12), *51473* (12); *Krapovickas 1251* (4a), *2586* (4a), *2906* (4a), *6681* (4a), *17861* (27), *25201** (4b), *34700** (30); *Krotkov 8709* (12); *Kuhlmann 2530* (11), *s.n.* (29).

L'Herminier s.n. (17); *Labat 1186* (8); *Ladd 12336* (12), *13859* (12); *Laferriere 2725* (18a); *Lanfranchi 186* (5), *453* (22), *481* (22); *Langlassé 263* (30); *Larez 605* (19); *Lasseigne 2812* (22); *Laughlin 1113* (1c); *Lawesson 3143* (1c); *Le Sueur 032* (1c), *12* (18a), *170* (18a), *173* (26); *Leavenworth & Hoogstrall 1335* (18a); *Leavenworth & Leavenworth 1335* (1c); *Leavenworth 199* (17), *442a* (30), *742* (15b), *966* (18a), *1371** (1a), *1453* (30), *1839* (8), *1875* (1c); *Ledru s.n.* (14); *Legaspi s.n.* (5); *Legrand 1455* (4a); *Lehmann 8745* (14); *Leino 76105* (17); *Lenaz s.n.* (11); *León 190* (9); *923* (9), *2532* (9), *2559* (9), *2674* (14), *3449* (9), *3747* (14), *3913* (17), *5681* (9), *6429* (14), *8834* (14), *9138* (14), *9314* (14), *9651* (9), *14181* (17), *15339* (14), *s.n.* (19); *Leonard 2030* (12), *4901** (14), *7449* (9), *7745* (14), *8344* (14), *9417* (14), *9607* (14), *11576* (9), *11875* (9), *11900* (9), *12237* (9), *12590* (9), *13147* (9), *13609* (9), *13744* (14), *13828* (9), *14338* (14), *15090* (9), *15754* (14), *16057* (12); *Leopold 109* (17), *176* (18a); *Levy 1018* (17); *Lewis 565* (4a), *629* (4a), *35344* (29); *Lindheimer 1266* (15b); *Lindmann A-1187* (27); *Liogier 21371* (22); *Lix 738* (5); *Lopez Figueiras 341* (14); *Lopez Miranda 951* (18a); *López Q. 26* (18a); *Lot 1948* (14); *Luces 17* (14), *188* (17); *Lundell 1335* (17), *7427* (14), *7622* (17), *7791* (14), *8719* (6), *10657* (15b), *14683* (6), *15918* (17); *Lyonnet 2639* (26); *Lyons Jr. 59* (1c), *83* (1c).

Martínez Crovetto 2 (4a), *8978* (27); *Macedo 2192* (11), *2194** (11); *Machado de Campos 209* (27); *Macnab 184* (9); *Macoun 26330* (12), *26331* (12), *26332* (12); *Macuszek 271* (5); *Magaña 427* (17); *Mally s.n.* (6); *Malme 3044* (11); *Malvárez 1350* (4a); *Mann 60* (15a); *Marsh 1278* (15a); *Martínez 1313* (1a), *6077* (4a), *7860* (17), *8272* (17), *8371* (17), *14613* (17); *Martínez Calderon 568* (17), *1798* (17); *Martínez F-1709* (15a), *F-2275* (15a), *F-2303* (15a), *F2333** (31), *F2364* (31); *Matuda 3577**** (17), *3640* (18a), *s.n.* (14); *McGregor 840* (1a), *870** (31); *McBride 332* (5), *3526* (18a); *McCarthy s.n.* (5); *McMurry 978* (16); *McVaugh 5164* (28), *16326* (18a), *16819* (20), *17705* (20), *19117* (18a), *19291* (1a), *19333* (18a), *19651* (20), *19578* (20), *20345**, ** (3), *21107* (26); *Mearns 738* (1c), *2294* (18a); *Medina 763* (17), *953* (17), *1246* (17); *Medrano F-1495* (18a); *Méndez 6220* (17); *Mengies 8023* (22); *Mereles 715* (30); *Metcalfe 1138* (5), *1442* (18a), *5511* (22); *Mexía 2740* (20), *5543a* (29), *5622** (11); *Meyer 33* (4a), *6329* (27); *Mick 44* (15a); *Miers 3429* (4a); *Miller s.n.* (12); *Moldenke 1372a* (5), *6377* (5); *Molina 242* (14), *2219* (17), *3905* (14), *15281* (17), *15426* (17); *Montaldo 3304* (19); *Montes 2018* (19), *3478* (4b), *11238* (27), *14642* (4a); *Monticelli 168* (22); *Moore Jr. 3924* (15a), *4218* (20); *Moraes 677* (24); *Moran 13664* (1c), *16483* (5), *18878 1/2* (1c); *Morel 7564* (4a), *8656* (4a); *Moreno 1181A* (18a), *9838* (1c), *21790* (18a), *21833* (18a); *Mori 243* (19); *Morley 696* (19); *Mosen 4469* (29); *Muelhenbach 667* (22); *Mueller 404* (30); *Mulford 1078* (18a); *Muller 987* (19), *s.n.* (19); *Muñoz 1006* (5); *Mutis 2151* (17); *Myers 4189* (17).

Nash 1297 (14); *Navarro s.n.* (22); *Nealley s.n.* (16), *s.n.* (1c); *Nease 71* (28); *Nee 183* (20), *6783* (17), *18347*

(17), *34307* (30), *37618* (4a); *Neill 1115* (19), *2454* (18a), *3910* (17); *Nelson 5621* (19), *6355* (18b), *s.n.* (17); *Nicora 1176* (4a), *2577* (4a), *2724* (4a), *2900* (4a), *6511* (5), *6806* (5), *8361* (22), *9737* (30), *18478* (30); *Noblick 3728* (30), *3955* (24); *Norton 339* (28); *Novara 8436* (22); *Noyes 459* (28).

O'Donell 2629 (30); *Ochoa 1584* (18a); *Orcutt 4197* (18a), *4687* (26); *Orihuela 92* (7), *s.n.* (7); *Ornelas U. 1167* (18a); *Oropeza s.n.* (17); *Ortíz 1049* (17).

Paget 152 (5); *Palacios 1856* (30), *4368* (4a); *Palmer 1c* (18a), *143* (18a), *168a* (30), *206*,*** (30), *208* (1a), *249* (1a), *251* (1a), *270* (30), *346* (1a), *525** (20), *533* (20), *554* (15a), *750* (1c), *802* (9), 1338 (15a), *1538* (30), *1545* (1c), *1554* (1c), *1657*** (26), *13277* (15a), *14147* (15a), *14214* (15b), *s.n.* (1c); *Parodi 590* (5), *607* (22), *1750* (5), *4490* (4b), *4512* (27), *4513* (27), *6935* (27), *8218* (5), *12363* (4a); *Pase 988* (15a), *1048* (15a), *1084* (18a); *Pastore 849* (22); *Pedersen 1882* (27), *3748* (4a), *5428* (27), *5457* (27), *5482* (27), *5812* (27), *11109* (27); *Peebles 7417* (1c), *10366* (18b); *Penn s.n.* (15a); *Pennell 3849* (17), *3866* (17), *20033* (3), *20221* (30); *Perez 8* (4a); *Peterson 6729* (17); *Pfister 60* (5); *Pickel 1393** (24), *1403* (4a), *3799* (11), *5154* (27), *5795* (27); *Pinheiro 36* (11), *55* (11), *74* (11), *182* (11), *218* (11), *265* (11), *273* (11), *297* (11), *336* (11), *362* (11), *382* (11), *385* (11), *483* (11), *530* (11), *561* (11), *512* (11), *581* (11), *587* (11), *596* (11), *603* (11), *634* (11); *Pinto 121* (24), *306** (24); *Piper 5253* (17), *s.n.* (15b), *s.n.** (6); *Pittier 2633* (14); *3441* (17), *3634* (17), *6332* (17), *6943* (17), *10534* (17), *10620* (17), *10830* (19), *12511* (19); *Plank 10* pr. p. (12), *12* (12), *38* (5), *57* (15a), *107* (12); *Plowman 8226* (29), *9269** (11); *Pohl 3885* (11), *10556* (14), *10653* (18a), *10944* (19), *11291* (19), *11437* (26), *11872* (18a), *12177*** (18a), *12210* (14), *Pohl 12228* (18a), *12369* (18a), *12674* (18a), *12707* (26), *13609** (18a), *13665* (18a), *13703* (19), *14172* (19); *Pollard s.n.* (16); *Popenoe 34* (17); *Porter s.n.* (12), *s.n.* (5); *Pott 444* (11), *3862* (11), *3915* (11); *Pringle 197* (1c), *376** (15a), *464* (1c), *497*,*** (20), *5573** (17), *13940** (1c), *s.n.* (30); *Proctor 2571* (30); *Purpus 6212* (18a).

Quarín 110 (4a), *1321* (22), *1639* (4a), *1969* (27), *2866* (27), *2909* (27); *Questel 1439* (14).

Ragonese s.n. (5); *Rambo 1937* (22), *9845* (4b), *9875** (7), *43391* (27), *43692* (27); *Ramia 3330* (17), *4444* (30), *4452* (30), *4831* (19), *5345** (30), *7201* (19), *8491* (30); *Ramírez 51* (30); *Ramírez Reyes 1715* (19), *1773* (19), *2048* (14), *2051* (17), *2054* (17), *2428* (14); *Reed 517** (14); *Reeder 1936* (14), *1956* (18a), *1962* (17), *2082* (1c), *2152* (26), *2164* (26), *2288* (26), *2300* (20), *2430* (1c), *3517* (18a), *3814* (20), *5520* (25), *6098* (1c), *6718* (1a), *7042* (8), *7045* (1a), *7425* (18a), *8630* (23); *Reeves P13125* (15a); *Reitz 17008* (22); *Renvoize 3583* (4a), *3637* (27), *3640* (4a), *3912* (30), *3933* (27), *4044* (27); *Reverchon 1842* (28), *2230* (15b), *2490* (15a), *2840* (16), *2841* (15a), *3527* (15a); *Reyes 34* (17); *Richard s.n.* (9); *Ricketson 677* (22); *Ridoult 1919* (18a); *Riedel 2155* (27), *s.n.* (29); *Robbin 860* (5); *Robleto 980* (18a), *1269* (18a), *1535* (18a); *Rodríguez 16* (19), *99* (4a), *541* (19), *694* (14), *1234* (19), *1981*** (19), *3056* (14), *3220* (14), *3126* (17), *3512* (22), *27191* (14); *Rodway s.n.* (17); *Rogers 4491* (15a), *4756* (15a), *6119* (15a), *6609* (6); *Rohweder 1497* (18a), *1648* (1c), *2507* (19); *Roig s.n.* (1c); *Rojas 105*** (4a), *2358* (4a), *2745* (29), *2762* (4a), *2784* (27), *5476a* (30), *6654* (29), *11027* (30), *11047* (30), *12741* (29), *12819* (29); *Roland 34* (12); *Rollins 5813* (15a); *Romanczuk 402* (4a); *Romero 190* (17); *Rondón 2585* (29); *Rose 1878* (30), *1883* (30), *1889** (30), *3281* (30), *4410* (9), *9555* (20), *18052* (15b), *69039* (16); *Rosengurtt B-242* (7), *B-480* (4a), *B-2228* (4a), *5411* (4a), *B-5623* (4a), *B-5829* (30), *B-681B* (4a), *B-7128* (7), *8893** (7); *Rotman 100*** (4a); *Roybal 867* (15a), *883* (15a); *Rúgolo 675* (5); *Ruíz 6* (5), *2468* (30); *Ruiz de Huidobro 459* (4a); *Ruíz Esparsa 208* (1c); *Ruíz Leal 5576* (22); *Runyon 1551* (14); *Rusby 444* (25); *Ruth 66* (12); *Rydberg 734* (16); *Rzedwosky 565* (20), *796* (20), *1136* (15a), *2047** (3), *3775* (20), *4539* (15a), *4618* (6), *4931* (15a), *5174* (15a), *6547* (15a), *6869* (15a), *17367* (3), *17423* (3), *17449* (3), *32145* (20), *39002* (8), *49933* (20), *49884* (8), *50000* (15a).

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Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 1995

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	20,162	2,145	22,307
Purchase	28,875	0	28,875
Exchange	28,773	3,006	31,779
Gifts	11,142	974	12,116
Total acquisitions	88,952	6,125	95,077
Mountings			
Newly mounted	56,158	12,534	68,692
Mounted when received	30,741*	0	30,741
Total specimens filed	86,899	12,534	99,433
Repairs			
Specimens repaired	29,948	n/a	29,948
Specimens stamped	3,973	n/a	3,973
Total repairs	33,921	0	33,921
Specimens sent			
On exchange	42,578	4,639	47,217
As gifts	23,083	783	23,866
Total	65,661	5,422	71,083
Loans sent			
Total transactions	642	54	696
Total specimens	40,439	9,534	49,973
To U.S. institutions			
Transactions	371	32	403
Specimens	25,491	4,989	30,480
To foreign institutions			
Transactions	271	22	293
Specimens	14,948	4,545	19,493
To student investigators			
Transactions	73	8	81
Specimens	11,067	513	11,580
To professional investigators			
Transactions	589	47	636
Specimens	29,372	9,021	38,393
Loans received			
Transactions	307	15	322
Specimens	22,713	1,877	24,590

* Of the 30,741 vascular plants "mounted when received," 28,875 are specimens of Chinese plants purchased directly from China.

	From U.S.	From abroad	Total
Visitors	336	85	421

On 31 December 1995 the total number of mounted, accessioned specimens in the herbarium was 4,591,434 (4,316,127 vascular plants and 275,307 bryophytes).

The 84,000 "mounted when received specimens" in the 1994 report should have been treated as purchases.—Marshall R. Crosby, *Senior Botanist.*

NOTICE

The 1995 Jesse M. Greenman Award

The 1995 Jesse M. Greenman Award has been won by Lynn Bohs for her publication "*Cyphomandra* (Solanaceae)," published as Monograph 63 of Flora Neotropica. This study is based on a Ph.D. dissertation from Harvard University under the direction of Dr. R. E. Schultes.

The Greenman Award, a certificate and a cash prize of $1,000, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1995 are now being accepted for the 28th annual award, which will be presented in the summer of 1996. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1995 award, reprints must be received by 1 June 1996.

Volume 83, Number 2, pp. 153–282 of the Annals of the Missouri Botanical Garden
was published on May 17, 1996.

Experimental and Molecular Approaches to Plant Biosystematics

The proceedings of the Fifth International Symposium of the International Organization of Plant Biosystematists (IOPB)

Edited by Peter C. Hoch and A. G. Stephenson

Twenty-three original contributions that span the breadth of biosystematics, a dynamic field of study that bridges the realms of systematics and population biology. The papers are arranged in four groups, reflecting the original four symposia of the 1992 meeting. *DNA and Plant Biosystematics* presents innovative work that uses the rapidly developing nucleic acid methods adapted from molecular biology. *Plant Growth Patterns and Biosystematics* includes comparative and developmental analyses of plant architecture and branching patterns. *Plant Reproductive Strategies* surveys new approaches in the analysis of plant reproductive biology, an area central to both systematic and population-level studies. *Phylogenetic Analysis and Population Biology* emphasizes the application of the powerful new methods of phylogenetic analysis to problems at the species and population levels. Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 53. ISBN: 0-915279-30-4. 416 pp. Illustrated. 1995. $60.00 U.S. $62.00 Non-U.S.

Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin*." Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

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A REVISION OF *CYNANCHUM* (ASCLEPIADACEAE) IN AFRICA[1]

Sigrid Liede[2]

ABSTRACT

Based on the study of dried specimens and living material, a taxonomic revision of *Cynanchum* in mainland Africa is presented. *Cynanchum* here comprises 31 species (about half the number found in Madagascar), 6 of them new. One new combination is proposed and two species are neotypified. An artificial key to all taxa is presented; all species are fully described, and taxa not previously illustrated are provided with illustrations. Names for African *Cynanchum* placed into synonymy under other genera are listed with their current placement.

Since the works of Schlechter (1895) and Brown (1902–1903, 1908), the African species of *Cynanchum* have not been revised. Asclepiadaceae have not been treated to date in most African Flora projects, with exception of Bullock (1963) for West Africa and Huber (1967) for Namibia. Therefore, even regional treatments of *Cynanchum* are lacking for most of the continent. The present account is the first one covering all of mainland Africa.

Vincetoxicum is understood as being separate from *Cynanchum* and is not considered here. There are only a very few species of *Vincetoxicum* in the extreme north and northeast of the African continent. The separation of *Vincetoxicum* renders irrelevant the question of whether *Blyttia* Arnold should be maintained for the treatment of *Cynanchum*, because *Blyttia* could possibly be subsumed under *Vincetoxicum*, but certainly not under *Cynanchum*. A more detailed account on the *Cynanchum*/*Vincetoxicum* problem is in preparation (Liede, in press).

To date, there is no valid infrageneric classification for *Cynanchum*. The present author recognizes only some East Asian members as sufficiently

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distinct to warrant sectional status (sect. *Rhodostegiella* (Pobed.) Tsiang & P. T. Li). All African members of the genus belong to the typical section *Cynanchum*.

In the course of a cladistic analysis, which will be published separately, it was found that the two presently recognized species of *Pentarrhinum* E. Mey., *P. abyssinicum* Decne. and *P. insipidum* E. Mey., are closely related to some species of *Cynanchum*, namely *C. balense* Liede, *C. gonoloboides* Schlechter, and *C. somaliense* (N. E. Br.) N. E. Br. Using morphological characters alone, however, evidence is not sufficient to either include *Pentarrhinum* in *Cynanchum* or to transfer the species mentioned to *Pentarrhinum*. The thick-walled follicles with protuberances, shared in Africa, as far as known, only by these five species, might constitute a stronger indication of relationships than the highly variable corona morphology. However, there are "true" *Cynanchum* species with muricate follicles in East Asia (*C. corymbosum* Wight, *C. muricatum* (Blume) Boerlage). The close relationship between *Cynanchum* and *Pentarrhinum* has been taken into account in the construction of the key, which includes the two presently recognized species of *Pentarrhinum*. As it was found during the course of this study that *Pentarrhinum* species were frequently labeled "*Cynanchum* indet." even in larger herbaria, this inclusion might also be of some practical value.

Materials and Methods

A total of ca. 2000 herbarium specimens from BM, BOL, EA, G, GRA, K, L, M, MAL, MO, NBG, P, PRE, SAM, SHRG, STEU, and UPS have been studied. Several collecting trips to Africa yielded living material of numerous species. Spirit material or restored material (heated to 65°C in Water:95% Ethanol:Glycerine = 5:4:1, plus 3 drops of detergent per 200 ml) was examined under a binocular microscope, and, in most cases, under the SEM after Critical Point Drying. Data have been stored in DELTA (version 3.06, Dallwitz, 1980; Dallwitz & Paine, 1986), and the descriptions were directly generated from this database. The key has been constructed manually using the INTKEY program for confirmation. Locality information has been derived from Polhill (1988) for East Africa and from various gazetteers for the remainder of Africa. Delimitation and spelling of subdivisions follows the guidelines for the major floras in the area; for East Africa (Kenya, Tanzania, Uganda), the subdivisions of the *Flora of East Africa* according to Polhill (1988) have been used (K1–K7, T1–T8, U1–U4, respectively). Throughout the paper, the corona terminology developed by Liede and Kunze (1993) has been used, in which Cs denotes the staminal parts of a gynostegial corona, Ci the interstaminal parts, and C(is) fused staminal and interstaminal parts. Indumentum terminology is following Hewson (1988).

Cynanchum L., Sp. Pl. 212. 1753. LECTOTYPE SPECIES: *Cynanchum acutum* L., designated by E. Meyer, Comm. Pl. Afr. Austr. 216. 1838.

Bunburia Harv., Gen. S. Afr. Pl. 416. 1838. TYPE: *Bunburia elliptica* Harv.

Colostephanus Harv., Gen. S. Afr. Pl. 417. 1838. TYPE: *Colostephanus capensis* Harv.

Cyathella Decne., Ann. Sci. Nat. Bot., sér. 2, 9: 332. 1838. Type species not designated.

Cynoctonum E. Mey., Comm. Pl. Afr. Austr. 215. 1838, not. J. F. Gmel. (1791). Type species not designated.

Endotropis Endl., Gen. Pl. 591. 1838, not Raf. (1825); nor Raf. (1838). Type species not designated.

Flanagania Schltr., Bot. Jahrb. Syst. 18, Beibl. 45: 10. 1894. TYPE: *Flanagania orangeana* Schltr.

Perianthostelma Baill., Hist. Pl. 10: 247. 1890. Type species not designated (*Perianthostelma abyssinicum* Baill., nomen nudum in schedis P).

Sarcocyphula Harvey, Thes. Cap. 2: 58. 1863. TYPE: *Sarcocyphula gerrardii* Harv.

Only synonyms relevant for mainland Africa have been considered.

Plants commonly twining, more rarely erect or decumbent, leafless or leafy; with milky, white to yellow latex; glabrous or with an indumentum; indumentum always consisting of uniseriate, multicellular hairs. *Inflorescences* usually bostrychoid, with geminiflorous partial inflorescences, basally occasionally with one or two dichasial ramifications; shortening of the rachis results in a sciadioidal inflorescence structure (inflorescence terminology following Weberling, 1989). *Flowers* 5-merous, small (not exceeding 1.5 cm diam., normally not exceeding 5 mm diam.); aestivation imbricate or contorted, always dextrorse. *Corolla* glabrous or adaxially with sparse, multicellular, verrucose trichomes. *Corona* present, of gynostegial origin, consisting of staminal (Cs) and interstaminal (Ci) parts fused for at least ¼ of total corona length (referred to as C(is) throughout this paper—corona terminology following Liede & Kunze, 1993); Cs, Ci, or both differentiated in shape; each lobe of Cs with or without adaxial appendage. *Anther wings* consisting of inner and outer ridges separated by a bristle-filled cavity, outer ridge either in the same plane as the back of the anther or centrifugal toward the base. *Pollinaria* consisting of two pendulous pollinia (synapomorphy of the tribe Ascle-

piadeae) and a well-developed translator apparatus. *Stylar head* with a conspicuous protrusion at the upper end of the corpusculum, dividing the stylar head in a rather uniform lower and a variable upper part. *Fruit* of two follicles, usually one aborted, follicles normally obclavate, winged or wingless, pericarp mostly thin and smooth, rarely thicker and/or with protuberances (see discussion above). *Seeds* brown, elliptic to pyriform in outline, winged or wingless, smooth, sculptured or hairy, crowned with a coma of white hairs. *Chromosome number*, as far as known, $2n = 22$. *Chemistry*: all species studied were found to contain pregnane glycosides.

Artificial Key to the Species of *Cynanchum* and *Pentarrhinum*

1. Plants twining, semi-succulent; without well-developed leaves 2
1′. Plants erect or twining, not succulent; with well-developed leaves 3
2(1). Staminal corona parts exceeding gynostegium and, in young flowers, connivent over it ..... *C. lenewtonii*
2′. Staminal corona parts not exceeding the gynostegium ..... *C. gerrardii*
3(1). Plants erect, rhizomatous, less than 30 cm high, sparsely branched to unbranched; leaves linear or at least three times longer than wide, corolla lobes with revolute margins; stylar head capitate 4
3′. Combination of characters otherwise 5
4(3). Leaves absent at the time of flowering; leaf blades 2–8 mm wide; inflorescences with well-developed rachis; caudicles flattened, straight ..... *C. praecox*
4′. Leaves present at the time of flowering; leaf blades less than 2 mm wide; inflorescences without well-developed rachis; caudicles cylindrical, s-shaped ..... *C. orangeanum*
5(3). Corolla lobes adaxially with trichomes 6
5′. Corolla glabrous 11
6(5). Corolla lobes only with a few basal smooth trichomes ..... *C. adalinae* subsp. *mannii*
6′. Corolla lobes with ± evenly spaced, verrucose trichomes 7
7(6). Staminal corona parts with adaxial appendages (ligules) 8
7′. Staminal corona parts without adaxial appendages (ligules) 10
8(7). Stylar head elongated, much exceeding the gynostegium ..... *C. umtalense*
8′. Stylar head not elongated, much shorter than the gynostegium 9
9(8). Leaves triangular; peduncles 2–10 mm long; inflorescences with rachis 0–0.5 mm long; corolla lobes not contorted in bud ..... *C. virens*
9′. Leaves ovate; peduncles 15–40 mm long; inflorescences with rachis 2–10 mm long; corolla lobes contorted in bud ..... *C. abyssinicum*
10(7). Plants less than 50 cm high, sparsely branched; leaves fleshy, less than 15 mm long, elliptic; corolla lobes less than 2 mm long; Cs and Ci fused for more than ¾ of corona length ..... *C. galgalense*
10′. Plants more than 2 m high, richly branched; leaves herbaceous to coriaceous, 20–40 mm long, ovate; corolla lobes more than 3 mm long; Cs and Ci fused for less than ½ of total corona length ..... *C. obtusifolium*
11(5). Staminal corona parts fused only at base; stylar head flat or umbonate; follicles thick-walled, warty or with soft spines 12
11′. Corona fused for at least ¼ of its length; stylar head of various shapes; follicles mostly thin-walled, smooth (except *C. gonoloboides*) 15
12(11). Corona of five fleshy, papillate, shining, yellow parts with appendages projecting toward the center of the flower ..... *Pentarrhinum insipidum*
12′. Corona not fleshy or papillate, without appendages projecting toward the center of the flower 13
13(12). Gynostegium stipitate; corona lobes prominently trifid ..... *C. somaliense*
13′. Gynostegium sessile; corona lobes not trifid 14
14(13). Leaves leathery, venation prominent, slightly cordate at the base; corona lobes bifid almost to the base ..... *C. balense*
14′. Leaves thin, venation not prominent, prominently cordate to lobate; corona lobes slipper-shaped ..... *Pentarrhinum abyssinicum*
15(11). Staminal corona with prominent adaxial appendages (ligules) 16
15′. Staminal corona without prominent adaxial appendages 17
16(15). Leaves at least abaxially with indumentum; inflorescences 20–35-flowered, rachis 15–60 mm long; peduncles 3–10 cm; corona not exceeding the gynostegium, interstaminal corona lobes shorter than staminal corona lobes; stylar head conical ..... *C. acutum*
16′. Leaves glabrous; inflorescences 1–12-flowered, rachis absent; peduncles ca. 1 cm; corona exceeding the gynostegium, staminal and interstaminal corona lobes of the same length; stylar head strongly bifurcate ..... *C. mossambicense*
17(15). Leaves hastate; corona papillose; stylar head elongate-conical to obinfundibuliform; follicles strongly obclavate and longly beaked 18
17′. Leaves not distinctly hastate; if triangular-deltate, then corona not papillose and stylar head not elongate-conical to obinfundibuliform; follicles not so strongly obclavate and less pronouncedly beaked 19
18(17). Stylar head well exceeding the corona; floral buds 6–6.5 mm long ..... *C. clavidens* subsp. *clavidens*
18′. Stylar head not or hardly exceeding the corona; floral buds 3–4 mm long ..... *C. clavidens* subsp. *hastifolium*
19(17). Corona fused for more than ¾ of its length 20

19′. Corona fused for less than ¾ of its length (strongly folded coronas appear more fused than they are, especially in *C. adalinae*, therefore check unfolded) 30
20(19). Mature leaves more than 5 cm long 21
20′. Mature leaves up to 5 cm long 22
21(20). Leaves dark green, with nerves raised abaxially; corona white, not obscuring the long-stipitiate gynostegium; follicles thick-walled, warty ..... *C. gonoloboides*
21′. Leaves lighter green, nerves not raised; corona purplish red, obscuring the sessile gynostegium; follicles thin-walled, smooth ..... *C. longipes*
22(20). Leaf blades about three times as long as wide, ovate, conspicuously paler below; gynostegium short-stipitate; stylar head umbonate, lower part of stylar head conspicuously bent upward in dried material ..... *C. rungweense*
22′. Leaf blades about twice as long as wide (in *C. falcatum* very rarely more than three times as long as wide, but then triangular or falcate), the same green above and below; gynostegium almost sessile to long-stipitate; stylar head conical or flat, but lower part not conspicuously bent upward in dried material 23
23(22). Plants erect shrublets; leaf blades less than 5 mm long, with margins thickened; corona apically papillose (10×); gynostegium sessile ..... *C. blyttioides*
23′. Plants decumbent or twining; leaf blades more than 5 mm long, margins not thickened; corona smooth throughout; gynostegium sessile or stipitate 24
24(23). Leaves strongly triangular, rarely falcate; Cs and Ci differentiated with the triangular Cs higher than the bifid Ci; stylar head clavate ..... *C. falcatum*
24′. Leaves ovate; corona either annular or with only Cs differentiated; gynostegium mostly on a bulge (sessile in *C. ellipticum*, almost sessile in some populations of *C. altiscandens*); stylar head not clavate 25
25(24). Corolla lobes conspicuously twisted in bud, more than 6 mm long; gynostegium long-stipitate (stipe > 2 mm) ..... *C. africanum*
25′. Corolla lobes not conspicuously twisted in bud, less than 5 mm long; gynostegium sessile or stipitate, but stipe shorter than 2 mm 26
26(25). Plants erect or twining; corona fused for about ¾ of its length 27
26′. Plants twining; corona almost totally fused 28
27(26). Plants dwarf shrublets or decumbent, but never twining; leaves rounded or indistinctly cordate at base, less than 1 cm long; corona not adnate to the filaments ..... *C. zeyheri*
27′. Plants twining; leaves distinctly cordate at base, more than 3 cm long; corona connate to the filaments ..... *C. schistoglossum*
28(26). Plants of coastal habitats; leaves fleshy; upper margin of corona neatly five-crenate, anther wings shorter than the anther ..... *C. natalitium*
28′. Plants not restricted to coastal habitats; leaves not fleshy; upper margin of corona smooth or irregularly crenulate, anther wings as long as the anther 29
29(28). Plants glabrous, mature plants forming a corky main stem, not sarmentose; peduncles 12–20 mm long; upper corona margin irregularly crenulate; gynostegium sessile (on a very short stipe in introgression forms with *C. natalitium*) ..... *C. ellipticum*
29′. Plants with indumentum (check the main nerves of the leaves, peduncles, and pedicels), sarmentose, not forming a corky main stem; peduncles 2–5 mm long; upper corona margin smooth; gynostegium mostly on a short bulge (almost sessile in some collections) ..... *C. altiscandens*
30(19). Plants erect shrublets, less than 50 cm high 31
30′. Plants twining, more than 1 m high 33
31(30). Leaves ovate, less than 20 mm long, base rounded, margins neither thickened nor crenulate ..... *C. meyeri*
31′. Leaves triangular, more than 25 mm long, base cordate to lobate, margins thickened and conspicuously crenulate 32
32(31). Corona fleshy, pink, Cs oblong, exceeding the gynostegium and Ci, Ci with conspicuously reflexed margins; anthers not massive ..... *C. rubricoronae*
32′. Corona not fleshy, white, Cs extended into a long, reflexed tip, margins of Ci straight; anthers massive ..... *C. crassiantherae*
33(30). Corona exceeding the gynostegium and totally obscuring it; Cs forming five conspicuous folds; stylar head conical; coma of the seeds attached along almost ⅓ of seed length 34
33′. Corona as long as the gynostegium or longer, but not obscuring it, Cs not forming folds; stylar head not conical; coma of seeds attached terminally 35
34(33). Inflorescences sessile or very shortly pedunculate (less than 1 cm) ..... *C. adalinae* subsp. *adalinae*
34′. Inflorescences long-pedunculate (more than 1.5 cm) ..... *C. adalinae* subsp. *mannii*
35(33). Corona as high as the gynostegium, or slightly higher 36
35′. Corona about twice as high as the gynostegium 37
36(35). Leaves cordate, but not lobate; corona adnate to the filaments for more than ⅓ of total corona length, lobes of Cs triangular, inflexed, upper margin variably toothed ..... *C. schistoglossum*
36′. Leaves lobate; corona not adnate to the filaments, staminal lobes oblong, erect, with involute margins ..... *C. ledermannii*
37(35). Corolla lobes more than 5 mm, corona more than 5 mm long; stylar head capitate ..... *C. polyanthum*
37′. Corolla lobes less than 5 mm, corona less than 5 mm long; stylar head umbonate ..... *C. heteromorphum*

1. Cynanchum abyssinicum Decaisne in Candolle, Prodr. 8: 548. 1844. *Vincetoxicum abyssinicum* (Decne.) Kuntze, Revis. Gen. Pl. 2: 424. 1891. TYPE: Abyssinica. *Quartin-Dillon s.n.* (holotype, G not seen). Figure 1.

Cynanchum abyssinicum var. *tomentosum* Oliver, Trans. Linn. Soc. London, Bot. 2: 342. 1887. TYPE: Tanzania. Kilimanjaro: Moshi, 1884, *Johnston 177* (lectotype, designated here, K).

Vincetoxicum holstii K. Schum., Bot. Jahrb. Syst. 17: 135. 1893. *Cynanchum holstii* (K. Schum.) K. Schum., Nat. Pflanzenfam. 4(2): 253. 1895. TYPE: Tanzania. Tanga: Mlalo, Usambara, *Holst 507* (holotype, B presumably destroyed; lectotype, designated here, K).

Plants ascending, twining, 3–4 m high, richly and irregularly branched. *Shoots* herbaceous, sparsely covered with appressed trichomes 0.5–0.7 mm long, along two lines, basally woody, with blackish bark (fide protologue of *Vincetoxicum holstii*); internodes 2.2–12 cm long, 0.9–1.5 mm diam. "*Stipules*" absent. *Leaves* with petioles 15–25 mm long, leaf blades herbaceous, 35–75 mm long, 10–35 mm wide, ovate, basally cordate, with 1–3 colleters in the adaxial sinus, apically acute to acuminate, adaxially isolatedly covered with appressed trichomes 0.35–0.4 mm long, evenly distributed over the whole surface to glabrous, abaxially slightly papillose, veins and margins isolatedly covered with appressed trichomes 0.35–0.4 mm long, to glabrous. *Inflorescences* bostrychoid, 15–20-flowered, 3–5 flowers open at a time; rachis 2–10 mm long. *Peduncles* 15–40 mm long, densely covered with appressed trichomes 0.1–0.5 mm long. *Flowers* sweetly scented (*Ash 2094, Maas Gesteranus 5161*); floral bracts 0.6–0.8 mm long, 0.1–0.2 mm wide at the base, triangular, with trichomes; pedicels 0.8–1.2 mm long, sparsely covered with erect trichomes 0.3–0.35 mm long. *Buds* 4.5–5 mm long, 1.6–1.7 mm diam., conical, with contorted aestivation. *Calyx* basally fused, ciliate, abaxial surface with trichomes; lobes 2.2–2.6 mm long, 0.8 mm wide, ovate, apically acute. *Corolla* rotate, basally fused; 6–7 mm long, abaxially and adaxially brownish purple, adaxially with verrucose trichomes 0.15–0.2 mm long, evenly distributed over the whole surface; lobes 1–1.2 mm wide, decurved, oblong, apically acute. *Corona* ivory, abaxially glabrous, 7–8 mm high, exceeding the gynostegium but not obscuring it; C(is) cyathiform, consisting of Cs and Ci fused for less than half of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, with adaxial appendages; lobes of Cs basally laminar, elongate-triangular, apically filamentous, flat to producing a convex fold, apically erect; appendages of Cs elongate-triangular, apically filamentous, erect. *Lobes of Ci* laminar, rectangular, bifid, or apiculate, producing a pronounced convex fold along the upper two-thirds of corona length, erect to reflexed, with straight, lacerate margins. *Gynostegium* 2 mm high, 1.6–1.8 mm diam., sessile. *Stamens* without free filaments; anthers about as high as broad, rectangular, abaxially planar; anther wings 1 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.8–0.85 mm long, 0.8–0.85 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.4–0.45 mm long, ovoid; caudicles 0.2–0.25 mm long, flattened, straight, horizontal, trapezoid; pollinia laterally attached to the caudicles, 0.5–0.55 mm long, 0.25–0.3 mm wide, ovoid, ovate in cross section. *Stylar head* cream, 1.5–1.7 mm diam., 1.1–1.3 mm high, upper part 0.8–1 mm high, depressed-conical. *Follicles* one per flower, pendulous, 70–75 mm long, 7–8 mm diam., obclavate, obtusely deltate in cross section, apically shortly beaked, irregularly keeled, dark brown, longitudinally grooved, glabrous. *Seeds* 5–5.5 mm long, 3–3.2 mm wide, pyriform, dark brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.6–0.8-mm-wide wing with entire margin; coma 25–30 mm long. (Description of follicles and seeds from the lectotype of var. *tomentosum, Johnston s.n.*) *Chromosome number* unknown.

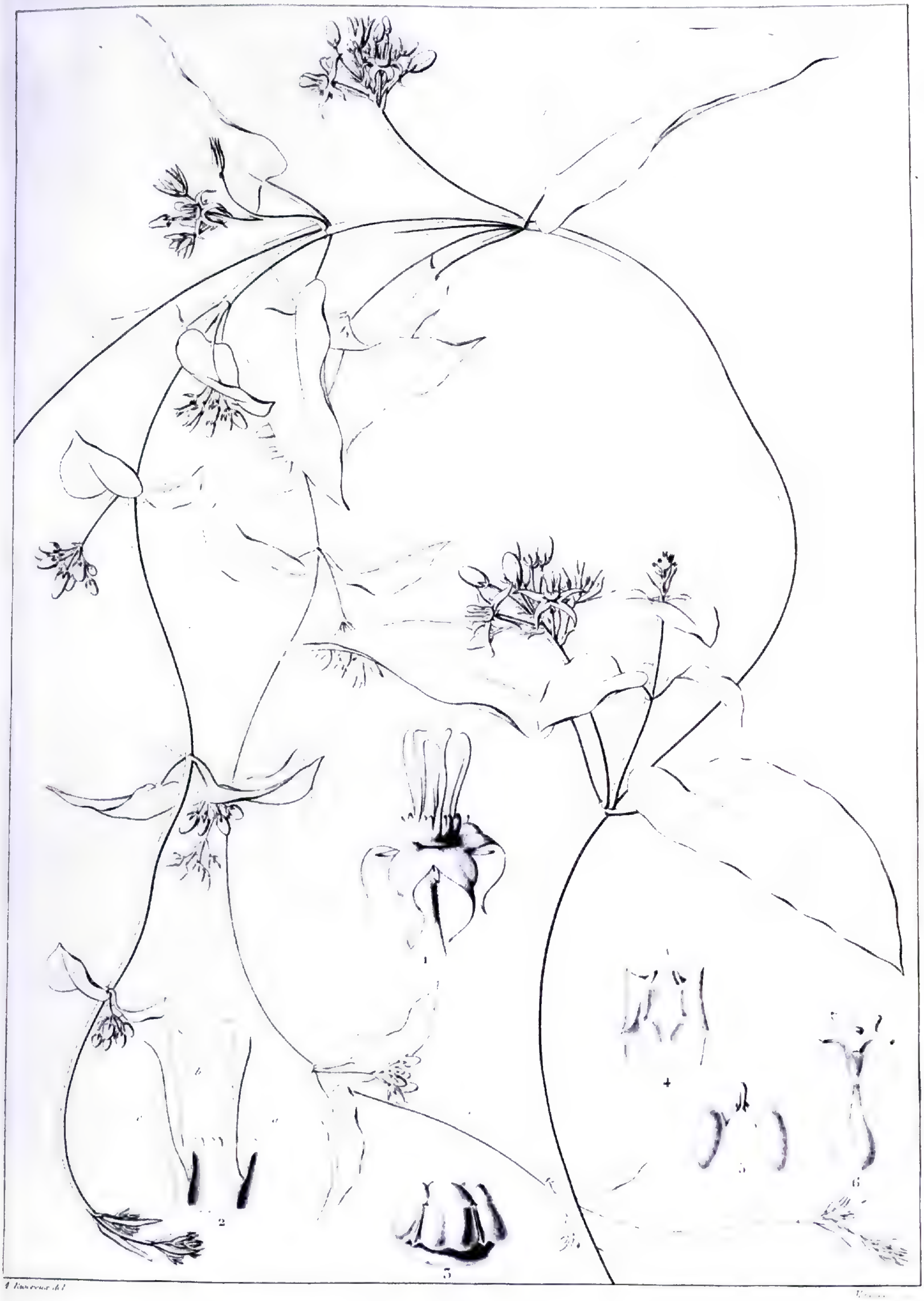
Distribution and habitat. Africa: Eritrea, Ethiopia (Arsi, Gonder, Ilubabor, Shewa, Welega), Kenya (K3, K4, K5, K7), Tanzania (T2, T3, T7), Uganda (U2), Zaïre; 1700–3000 m; forest margins, savanna, open scrub, often in secondary vegetation. Widespread, but infrequent. Figure 2.

Flowering time. All year, with peak between June and October.

Vernacular names. Maneriat (Kipsangali).

Uses. Used as a relish (*Perdue & Kibura 11341*); leaves used to make tea as a tonic (*Matthews 6354*).

Selected specimens examined. ERITREA. Dekemehare, 2000 m, *Schimper s.n.* (UPS). ETHIOPIA. **Arsi:** Chilalo awraja, N slope of Mt. Chilalo, 2900 m, 20 Nov. 1971, *Thulin 1522* (K, UPS). **Gonder:** Fenter, 12 Dec. 1909, *Chiovenda 1450* (FT). **Ilubabor:** Kombolcha, 2050 m, 12 Dec. 1960, *Mooney 8789* (K). **Shewa:** Addis Ababa, Entoto ridge above Italian Embassy, 2550–2600 m, 18 Sep. 1975, *Gilbert & Thulin 1001* (K, MO, UPS). **Welega:** about 5 km E of Lekemti, ca. 1800 m, 13 Nov. 1965, *De Wilde & De Wilde-Duyfjes 8843* (K, MO, UPS). KENYA. **Central:** Machakos, Chyulu North, 1800 m, 22 Apr. 1938, *Bally 7934*



CYNANCHUM abyssinicum. *Dne.*

DC. Prodr. vol 8. pag. 548.

Figure 1. *Cynanchum abyssinicum* Decne. Illustration from De Lessert, Icones plantarum. Vol. 5, Tab. 69.

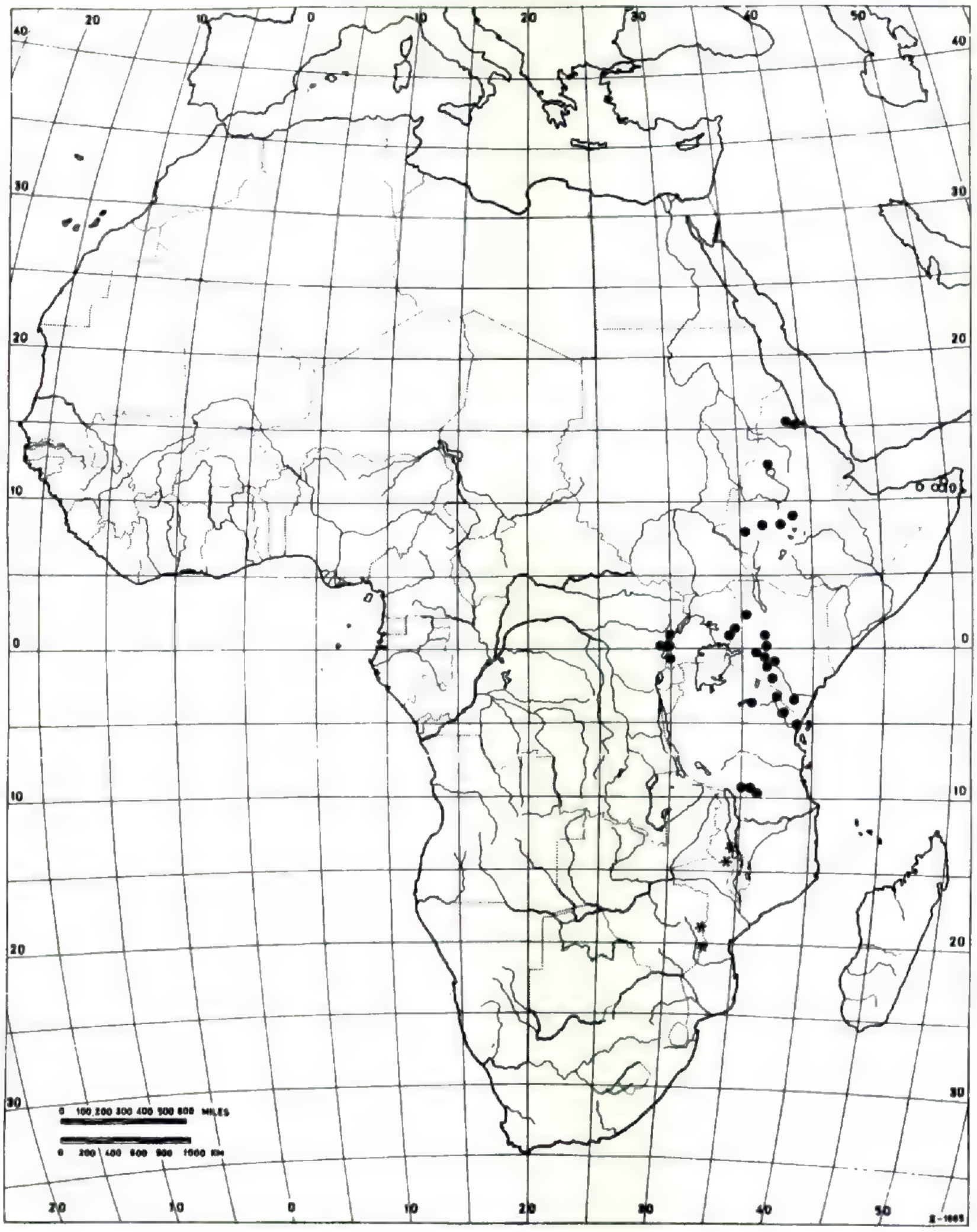


Figure 2. Known distribution of *Cynanchum abyssinicum* (dots), *C. galgalense* (open circles), and *C. umtalense* (asterisks).

(K); North Nyeri, Nyeri, 2000 m, 30 Jan. 1933, *Napier 2495* (K); South Nyeri, Kiandongoro forest, Nyeri-Naivasha rd., ½ mi. from Kagumo bridge, 21 Aug. 1968, *Mathenge 376* (MO). **Nyanza:** Londiani, Tinderet Forest Reserve, Camp 2, 2400 m, 22 June 1949, *Maas Gesteranus 5161* (K). **Rift Valley:** Naivasha, S of Kinangop, 3000 m, 22 July 1961, *Polhill 433* (EA, K); Nakuru, Nyahururu, ca. 15 km N of Thompson Falls, 23 Aug. 1981, *Gilbert 6345* (EA, K); Trans Nzoia, E of Mt. Elgon, 2830 m, 8 Jan. 1955, *Irwin 180* (K). TANZANIA. **Arusha:** Oldeani Mt., 2000 m, 10 Feb. 1932, *St. Clair-Thompson 612* (K). **Iringa:** Mufindi, escarpment above Luisenga stream, 1600 m, 17 Aug. 1984, *Bridson & Lovett 533* (K, MO). **Tanga:** Marungu, 1600 m, July 1893, *Volkens 641* (K). UGANDA. Kigezi, Elephant Valley, 2330 m, 11 Mar. 1960, *Lind 2710* (K); Mbale, Buginyanya, Bugishu, 2000 m, 1 Sep. 1932, *Thomas 464* (K). ZAÏRE. Biega-Kivu Mts., 1929, *Humbert 7604* (K); entre Kibati et Miragongo, Mission au Parc National Albert, Jan. 1938, *Lebrun 9391* (K).

Comments. The degree of hairiness varies greatly between densely tomentose and almost glabrous. As there is neither a sharp limit between glabrous and hairy forms nor a correlation with other characters, the separation of variety *tomentosum* Oliver does not seem advisable. This variety has never been properly published, but its name is frequently found on specimens. The specimen selected as lectotype is marked as type by N. E. Brown, but was not cited as such in, e.g., *Flora of Tropical Africa* (Brown, 1902–1903).

Cynanchum abyssinicum is most closely related to *C. umtalense* and *C. virens*, with which it shares the trichomes on the adaxial corolla surface and the ligulate corona.

2. Cynanchum acutum Linnaeus, Sp. Pl. 212. 1753. *Vincetoxicum acutum* (L.) Kuntze, Revis. Gen. Bot. 2: 424. 1891. *Solenostemma acutum* (L.) Wehmer, Pfl.-Stoffe, ed. 2, 2: 1004. 1931. TYPE: LINN 308/3 (holotype, LINN). Figure 3.

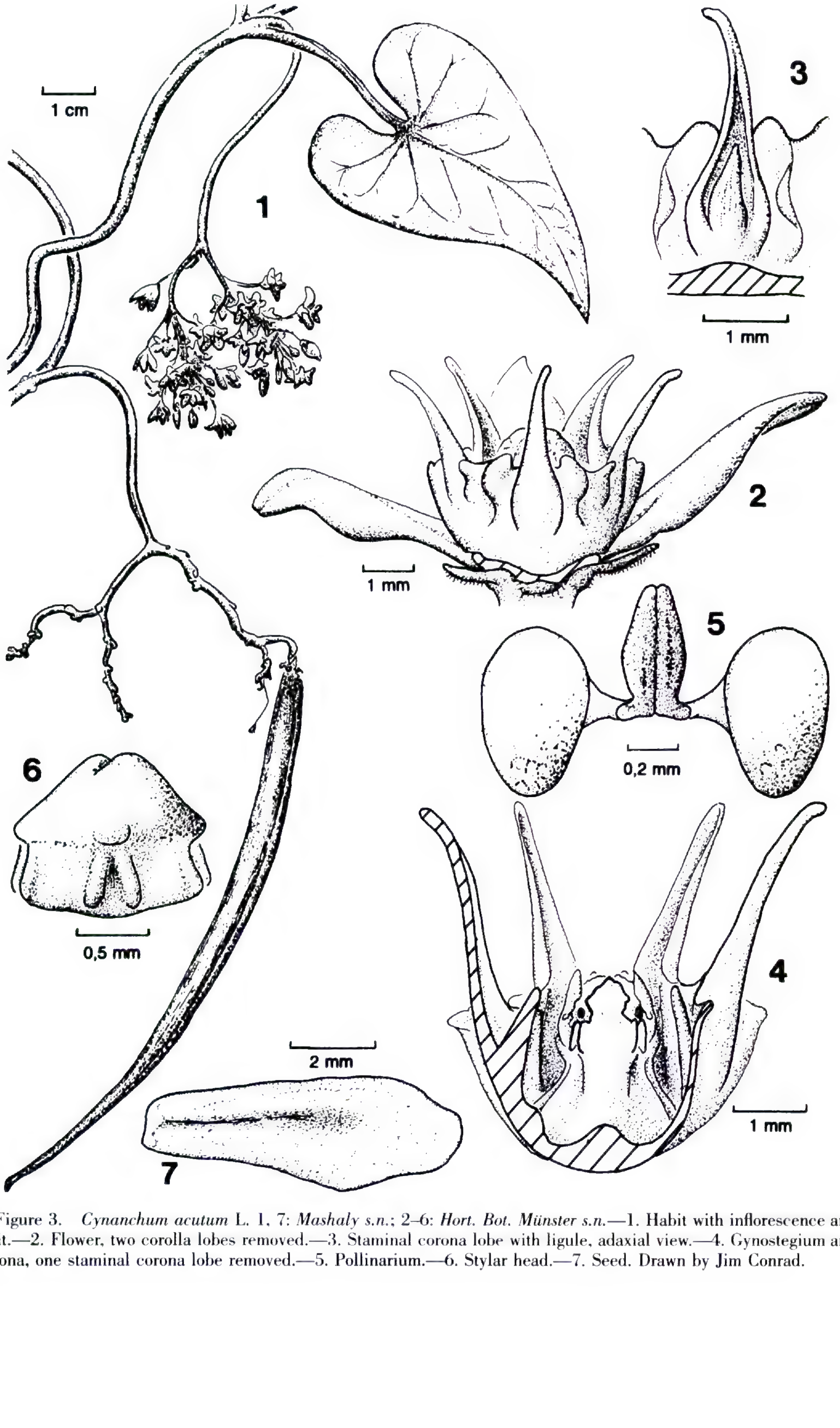


Figure 3. *Cynanchum acutum* L. 1, 7: *Mashaly s.n.*; 2–6: *Hort. Bot. Münster s.n.*—1. Habit with inflorescence and fruit.—2. Flower, two corolla lobes removed.—3. Staminal corona lobe with ligule, adaxial view.—4. Gynostegium and corona, one staminal corona lobe removed.—5. Pollinarium.—6. Stylar head.—7. Seed. Drawn by Jim Conrad.

Cynanchum excelsum Desf., Fl. Atlant. 1: 212. 1798. *Vincetoxicum excelsum* (Desf.) Kuntze, Revis. Gen. Pl. 2: 424. 1891. TYPE: Tunisia. Tozzer, *Desfontaines 489* (holotype, P).

Cynanchum fissum Pomel, Nouv. Mat. Fl. Atl. 81. 1874. TYPE: Algeria. Berges du Chellif, *Pomel s.n.* (holotype, AL not seen; isotype, P).

Cynanchum monspeliacum L., Sp. Pl. 212. 1753. TYPE: LINN 308/6 (holotype, LINN).

Only synonyms relevant for Africa have been considered.

Plants ascending, twining, richly branched. *Shoots* herbaceous, sparsely to densely covered with flexuous trichomes 0.5–0.75 mm long; internodes 6–15 cm long, 1.5–2 mm diam. "*Stipules*" absent. *Leaves* with petioles 15–50 mm long; leaf blades herbaceous, 45–60(–70) mm long, 25–45(–70) mm wide, triangular, basally cordate to lobate, lobes 13–20 mm long, with 1–3 colleters in the adaxial sinus, apically obtuse, with flexuous trichomes 0.5–0.6 mm long, evenly distributed, abaxially isolatedly covered with flexuous trichomes 1–1.2 mm long, restricted to veins and margins. *Inflorescences* 20–35-flowered, 10–24 flowers open at a time, basally dichasial, apically bostrychoid, rachis 15–60 mm long. *Peduncles* 30–100 mm long, sparsely to densely covered with flexuous trichomes 0.8–1 mm long. *Flowers* with a sweetish carnation-like scent, very nectariferous; floral bracts 1.5–2 mm long, 0.4–0.6 mm wide at the base, ovate (–lanceolate), glabrous; pedicels 7–25 mm long, densely covered with flexuous trichomes 0.4–0.6 mm long. *Buds* 5–6 mm long, 2.5–3 mm diam., conical, with contorted aestivation. *Calyx* basally fused, abaxial surface with trichomes; lobes 2.2–2.5 mm long, 1.1–1.3 mm wide, ovate, apically acute. *Corolla* rotate, basally fused, 5–8 mm long, abaxially rose, adaxially basally purple, apically rose; lobes 1–1.3 mm wide, twisted, patent to horizontal, oblong, apically obtuse. *Corona* pink, 2.7–3 mm high, shorter than the gynostegium; C(is) consisting of Cs and Ci fused for about two-thirds of total corona length, Cs and Ci differentiated, Ci slightly shorter than Cs. *Cs* basally just adnate to the filaments, appressed to the back of the stamens, with adaxial appendages; lobes of Cs laminar, triangular, apically erect; appendages of Cs slightly longer than Cs, laminar, triangular, erect. *Lobes of Ci* laminar, deeply bifid, producing a cleft in front of the guide rails and a pronounced convex fold along the upper two-thirds of corona length, erect, with straight margins. *Gynostegium* 3.2–3.5 mm high, 2.5–2.7 mm diam., sessile. *Stamens* with free filaments 0.5–0.6 mm long; anthers about as high as broad, rectangular, abaxially planar. Anther wings 1.2–1.5 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.5–0.6 mm long, 0.5–0.6 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.3–0.35 mm long; caudicles 0.1 mm long, flattened, straight, horizontal, triangular; pollinia laterally attached to the caudicles, 0.35–0.4 mm long, 0.35–0.4 mm wide, globose, elliptical in cross section. *Stylar head* 1.4–1.5 mm diam., 1.1–1.2 mm high; upper part 0.7–0.75 mm high, depressed-conical. *Follicles* usually one per flower, pendulous, 80–150 mm long, 7–8 mm diam., fusiform to narrowly oblong, round in cross section, apically strongly beaked, light brown, longitudinally grooved, glabrous. *Seeds* 6–6.5 mm long, 2.8–3 mm wide, ovate, light brown, seta and aseta side sculptured with longitudinal ridges, marginally with wing 0.3–0.4 mm wide with entire margin; coma 30–35 mm long. *Chromosome number*: $2n = 22$ (voucher: *ex hort. Münster s.n.*, MSUN).

Distribution and habitat. Asia. Europe. Africa: Algeria, Egypt, Tunisia; lowlands, close to water. Very widespread and not rare, but uncommon in Africa. Figure 4.

Flowering time. September to October.

Additional specimens examined (Africa only). EGYPT. Kom Aushim, El Fayum, 15 July 1960, *Boulos s.n.* (G); Bords de Nil à Kasr-el-Aïm près le Caire, 13 Oct. 1908, *Burdet 481* (G); Culhares à Koubak, 20 m, 21 Oct. 1908, *Burdet 482* (G); Damietta, Ezbit-El-Burg, 18 Oct. 1982, *Mashaly s.n.* (K); Aegypto superiori, 1837, *Schimper 959* (L). TUNISIA. Gafsa, Feb. 1908, *Pitard 434* (L).

Comments. This is the lectotype species of *Cynanchum,* designated by E. Meyer (1838). This Eurasian taxon extends into Africa only at the northern margins. Sometimes, infraspecific taxa are recognized under this widespread and variable species; none of them, however, is based on African material. Among African species, *C. mossambicense* is probably the closest relative.

3. Cynanchum adalinae (K. Schumann) K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 253. 1895. *Vincetoxicum adalinae* K. Schum., Bot. Jahrb. 17: 134. 1893. TYPE: Gabon. Ogowe, 10 Apr. 1881, *Soyaux 277* (holotype, B presumably destroyed; lectotype, designated here, K). Figure 5.

Plants ascending, twining, 2.5–5 m high, richly and irregularly branched; rhizomatous; rhizomes 2–3 mm diam. *Shoots* perennial, herbaceous, sparsely

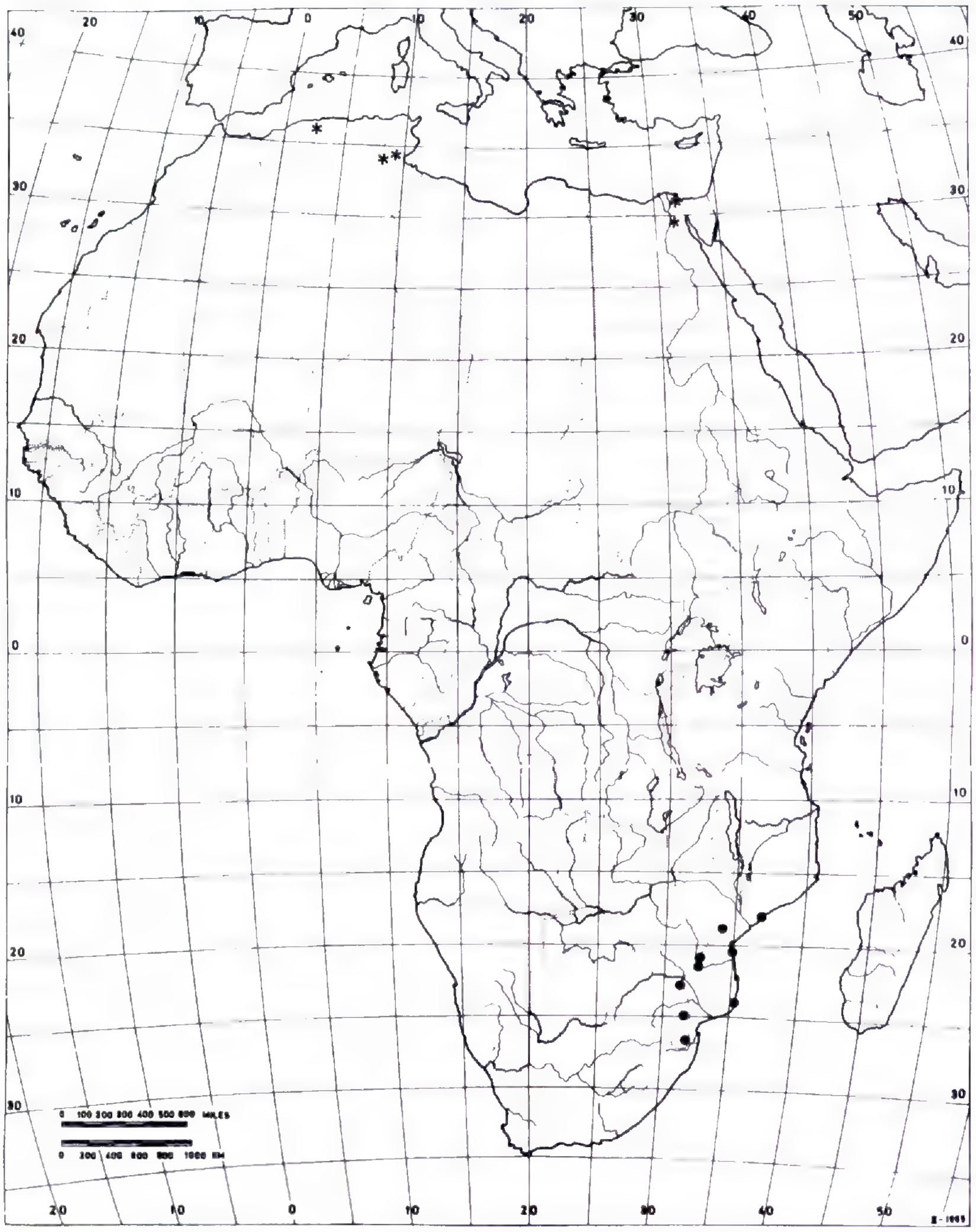


Figure 4. Known distribution of *Cynanchum acutum* (asterisks) in Africa, and of *C. mossambicense* (dots).

covered with flexuous trichomes 0.2–0.25 mm long, along a single line, basally woody, with brownish bark; internodes 7–15 cm long, 1–1.5 mm diam. "*Stipules*" absent. *Leaf blades* herbaceous to papery, ovate to elliptic, apically acuminate, apiculus 6–10 mm long, adaxially and abaxially glabrous. *Inflorescences* 15–25-flowered, 5–9 flowers open at a time, basally frequently with one or two bifurcations, apically bostrychoid. *Flowers* sweetly scented (*Breteler 1287*); floral bracts triangular, glabrous; pedicels 3–6 mm long, densely covered with flexuous trichomes 0.15–0.2 mm long, along a single line. *Buds* conical, basally with imbricate, apically contorted aestivation. *Calyx* rotate, basally fused, ciliate, lobes ovate, apically acute. *Corolla* rotate, basally fused, abaxially and adaxially creamish green, lobes incurved to patent, oblong to lanceolate. *Corona* white, 2.5–3 mm high, exceeding the gynostegium, almost entirely obscuring it; C(is) consisting of Cs and Ci fused for ½ to ¼ of total corona length, Cs and Ci differentiated, Ci longer than Cs. *Cs* not adnate to the filaments, appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, oblong, producing a pronounced convex fold, apically inflexed, with straight margins. *Lobes of Ci* laminar, oblong (when flattened), producing a pronounced convex fold along the upper two-thirds of corona length resulting in a cucullate shape, erect, with straight margins. *Gynostegium* 1.6–1.8 mm high, 1.5–1.6 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, trapezoidal, abaxially planar; anther wings 0.9–1.1 mm long, convergent, extending along the whole length of the anther, stamens forming a triangular basal arch; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.6–0.8 mm long, 0.3–0.35 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum

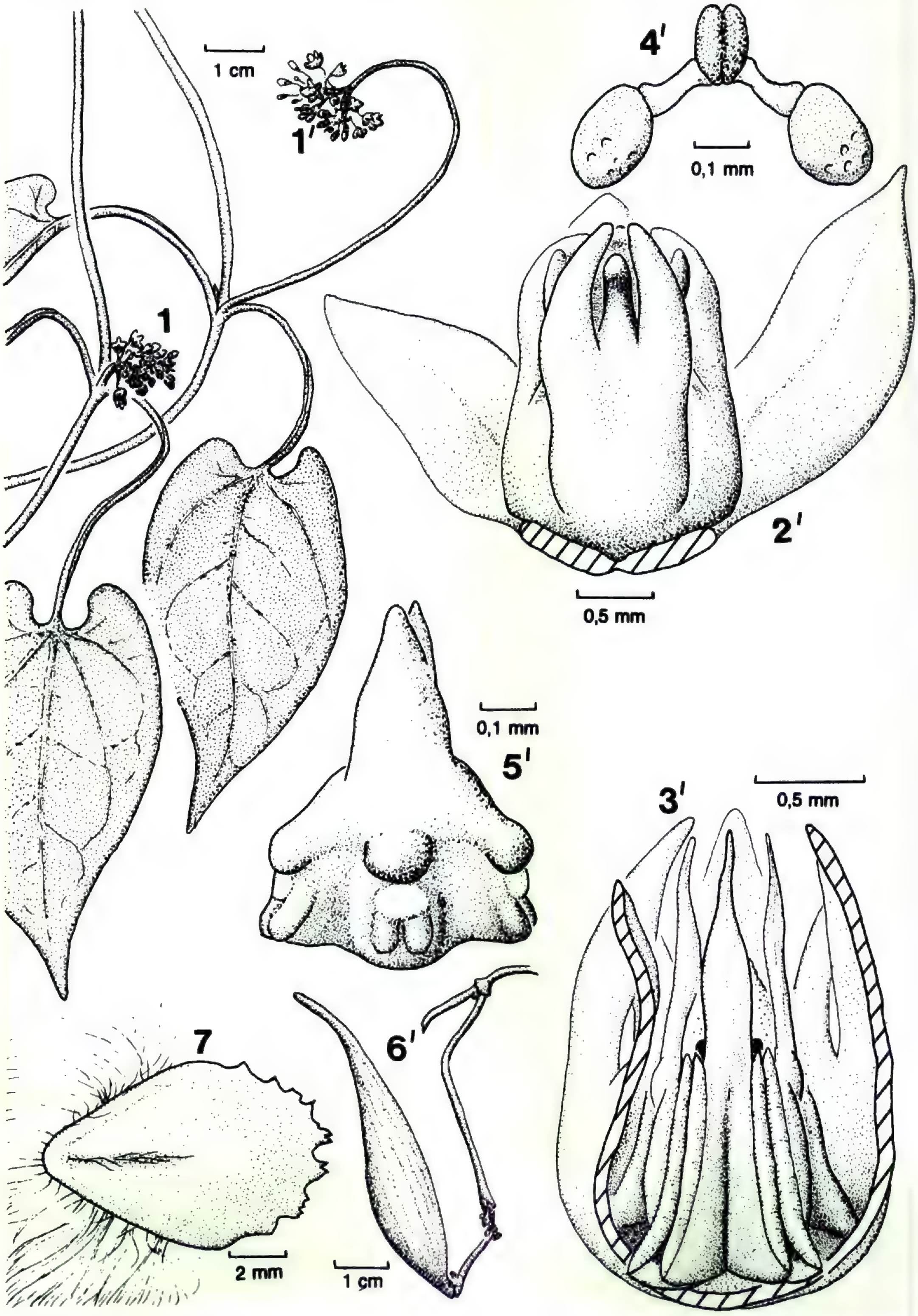


Figure 5. *Cynanchum adalinae* (K. Schum.) K. Schum. 1, 7: subspecies *adalinae* (*Morton s.n.*). 1′–6′: subspecies *mannii* (Scott-Elliott) Bullock. 1′–5′: *Bos 1832*; 6′: *Deighton 2522*.—1, 1′. Internodes and inflorescences.—2′. Flower, two corolla lobes removed.—3′. Gynostegium and corona, partially removed.—4′. Pollinarium.—5′. Stylar head.—6′. Fruit.—7. Seed, seta side; note the attachment of the coma, which is unique in the genus. Drawn by Jim Conrad.

0.18–0.2 mm long; caudicles 0.12–0.15 mm long, cylindrical, straight, declinate, thickened at the insertion of the pollinium; pollinia apically attached to the caudicles, 0.14–0.16 mm long, 0.13–0.15 mm wide, globose, elliptical in cross section. *Stylar head* white, 0.75–0.8 mm diam., 0.95–1 mm high; upper part 0.65–0.7 mm high, conical. *Follicles* one, occasionally two per flower, pendulous, 60–95 mm long, 7–10 mm diam., fusiform, round to obtusely deltate in cross section, apically strongly beaked, keeled, medium brown with green mottling, longitudinally grooved, glabrous. *Seeds* 8.5–9.5 mm long, 5.5–6 mm wide, ovate, light brown, seta and aseta side sculptured with longitudinal ridges, marginally with wing 0.8–1.2 mm wide, distally with irregular, strongly dentate margin; coma 25–30 mm long, attached to the seed along about one-third of its length.

Comments. The affinities of *Cynanchum adalinae* are still uncertain; the closest relative is most likely among *C. altiscandens* and its relatives.

KEY TO THE SUBSPECIES:

Inflorescences sessile or very shortly pedunculate (less than 1 cm)..... *C. adalinae* subsp. *adalinae*
Inflorescences long-pedunculate (more than 1.5 cm)..... *C. adalinae* subsp. *mannii*

3a. **Cynanchum adalinae** subsp. **adalinae**

Cynanchum congolense De Wild., Ann. Mus. Congo, Sér. 5, 1: 190. 1903–1906. TYPE: Congo. Wangata, *Defève 644* (holotype, not found).

Leaves with petioles 15–30 mm long; leaf blades 50–75 mm long, 30–50 mm wide, basally cordate to lobate, lobes 6–11 mm long, with 1–2 colleters in the adaxial sinus. *Inflorescences* sessile to very shortly pedunculate (peduncles to 6 mm long); rachis 2–4 mm long. *Floral bracts* 0.6–0.7 mm long, 0.7–0.8 mm wide at the base. *Buds* 2.5–3 mm long, 1.5–1.8 mm diam. *Calyx* lobes 0.8–1 mm long, 0.5–0.6 mm wide. *Corolla* 3.5–4 mm long, lobes 1.5–1.8 mm wide, apically acute. *Chromosome number*: $2n = 22$ (voucher: *Meve 903*, MSUN).

Distribution and habitat. Africa: Cameroon, Congo, Fernando Po, Gabon, Ghana, Ivory Coast, Nigeria, Zaïre; 6–650 m; edges and openings of secondary forest. Widespread. Figure 6.

Flowering time. December to September.

Selected specimens examined. CAMEROON. Kribi, ca. 13 km on Ebolowa rd., 14 Nov. 1968, *Bos 3277* (K, MO, WAG); Bertoua, near Catholic mission, ca. 650 m, 25 Apr. 1961, *Breteler 1287* (K, WAG); Oveng, near village, 27 km from Sangmélima along rd. to Yaoundé, 20 Mar. 1962, *Breteler 2654* (K, WAG); Victoria, July 1904, *Kalbreyer 3* (K); Mt. Cameroon, above Likombe, 900 m, 27 Feb. 1995, *Meve 903* (MSUN). CONGO. Léfini, Région de Kindamba, environs de Meya, sur la piste d'Hamon, ca. 100 m, 4 Nov. 1963, *Descoings 11307* (MPU). FERNANDO PO. 1861, *Mann s.n.* (K). GABON. Estuaire, Forest de la Mondah, rd. from Libreville to Santa Clara, 16 Sep. 1986, *Breteler, Lemmens & Nzabi 7769* (WAG); N'gounié, Waka, ca. 380 m, 24 Nov. 1984, *Arends, Louis & De Wilde 440* (WAG); Ogoué, about 15 km SSE of Pana, 19 Oct. 1983, *Breteler 6983* (WAG). GHANA. **Ashanti:** Mampong, 8 Dec. 1953, *Morton 75* (K). **Central Region:** Cape Coast, 6 m, 7 July 1959, *Hall 1513* (K). IVORY COAST. 2 km à l'Est de Rubino, 18 June 1963, *Garnier & Bouaké 18* (K); ca. 16 km NW of Sassandra, near Gunther Fuyts house, on Pont de Neuve, c. 4 km SE of Louga, 13 June 1963, *De Wilde 200* (K, WAG). NIGERIA. Benin, Sapoba Forest reserve, near Abé village, ca. 5 mi. from Sapoba on Sapele rd., P.S.P. 89, 28 June 1957, *Onochie 36654* (K). **Lagos:** 70 mi. E of Lagos, *Lamborn 303* (K); Ogoya. Ikom/Obudu div., ca. ¼ mi. SW of Boje enclave P 43, Afi River reserve, 28 May 1946, *Jones & Onochie 18918* (K). **Ondo:** Akure, Idanre, ca. 500 m, 3 Mar. 1948, *Brenan & Keay 8691* (K). ZAÏRE. Yangambi Plateau, Italowe, 9 Sep. 1938, *Louis 1265* (SHRG).

Comments. The type of *Cynanchum congolensis* De Wild. has not been found. The fairly detailed description, however, leaves no doubt that the specimen described belongs to *C. adalinae* subsp. *adalinae*. The main differences noted are the slightly smaller flowers and the almost sagittate leaf bases. As both floral size and leaf shape tend to be slightly variable, there is no reason to maintain *C. congolensis* as distinct.

3b. **Cynanchum adalinae** subsp. **mannii** (Scott-Elliott) Bullock, Kew Bull. 17: 185. 1963. *Vincetoxicum mannii* Scott-Elliott, J. Linn. Soc., Bot. 30: 93. 1894. *Cynanchum mannii* (Scott-Elliott) N. E. Br. in Dyer, Fl. Trop. Afr. 4(1): 394. 1903. TYPE: Sierra Leone. Bagroo River, 1861, *Mann s.n.* (holotype, K).

Cynoctonum acuminatum Benth. in Hook., Niger Fl. 453. 1849. *Cynanchum acuminatum* (Benth.) K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 253. 1895, non *Cynanchum acuminatum* Humb. & Bonpl. ex Schult, Syst. Veg. 6: 111. 1820. TYPE: Sierra Leone. *Don s.n.* (holotype, BM not seen).

Leaves with petioles 25–35 mm long; leaf blades 55–65 mm long, 20–30 mm wide, ovate to elliptic, basally cordate with 3–4 colleters in the adaxial sinus. *Inflorescences* with peduncles 15–65 mm long; rachis 5–15 mm long. *Floral bracts* 0.5–1.2 mm long, 0.4–0.6 mm wide at the base. *Buds* 3–4 mm long, 1.5–1.8 mm diam. *Calyx* lobes 1.2–1.4 mm long, 0.6–0.7 mm wide. *Corolla* 3–4 mm long, adaxially basally sometimes with a few smooth trichomes; lobes 1–1.2 mm wide, apically obtuse.

Distribution and habitat. Africa: Ivory Coast,

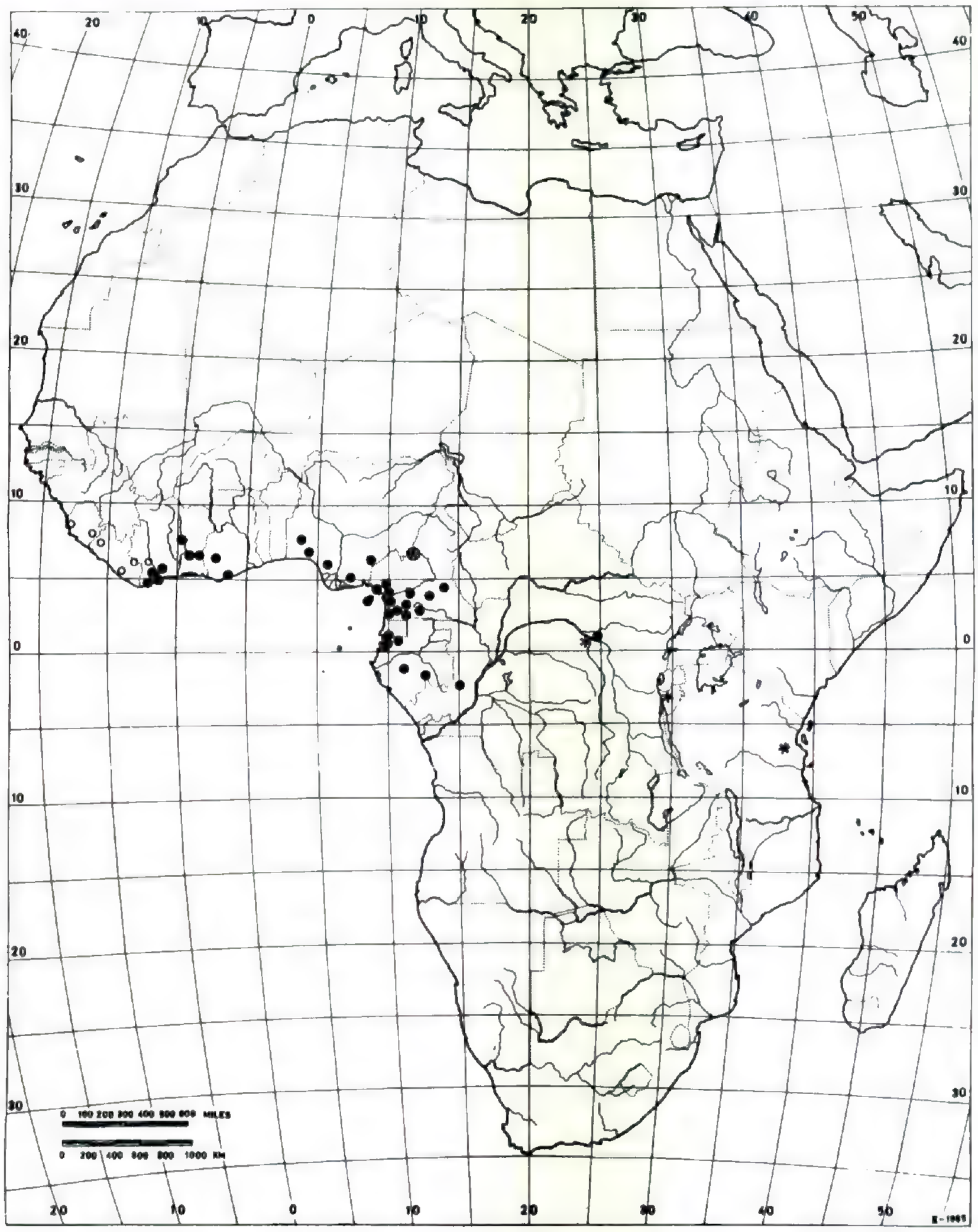


Figure 6. Known distribution of *Cynanchum adalinae* subsp. *adalinae* (dots), subspecies *mannii* (open circles), and *C. ledermannii* (asterisks). The one traced locality of one of the lost types is indicated by a circle around the asterisk.

Liberia, Sierra Leone; 50–200 m; edges and openings of primary forest. Not as widespread and frequent as the typical subspecies, but not immediately endangered. Figure 6.

Flowering time. February to October.

Selected specimens examined. IVORY COAST. 25 km SW of Guéyo, ca. 100 m, 26 Mar. 1962, *Leeuwenberg 3738* (K, MPU, WAG). LIBERIA. Grand Bassa, 20 mi. N of Buchanan, 18 Jan. 1969, *Jansen 1914* (WAG); Grand Gedeh, about 5 mi. S of Tchien, on rd. to Sinoe, 18 Jan. 1969, *Jansen 1244, 1245* (WAG); Montserrado, road from Bomi Hills to Gbama, 120 km from Monrovia, 18 Oct. 1963, *Van Harten 165* (K, WAG). SIERRA LEONE. **Southern Province:** Vevehun, between Fwendu and Potoru, 11 Apr. 1929, *Deighton 1649* (K). **Western Area:** Havelock, Freetown, 19 June 1964, *Morton 1368* (K, MO, WAG).

Comments. Distinguished from the typical subspecies mainly by the much longer peduncle. Found in the western part of the distribution area of the species.

Cynanchum dinklagei Schltr. ex Milbr. [Repert. Spec. Nov. Regni. Veg. 41: 264. 1937, nomen nudum] represents this taxon, judging from original material (*Dinklage 3064*, K).

Cynanchum adalinae subsp. *mannii* is illustrated in Adam (1975: 971, pl. 505).

4. **Cynanchum africanum** (Linnaeus) Hoffmannsegg, Verz. Pfl.-Kult. 54. 1824. *Periploca africana* L., Sp. Pl.: 212. 1753. *Vincetoxicum africanum* (L.) Kuntze, Revis. Gen. Pl. 2: 422. 1891. *Periploca pallida* Salisb., Prodr. Stirp. Chap. Allerton 148. 1796, nom. superfl. (renaming of *P. africana* L.). TYPE: *H.S.C. 79* (lectotype, designated by Wijnands (1983), BM not seen).

Cynanchum crassifolium R. Br., Mem. Wern. Nat. Hist. Soc. 1: 46. 1810. *Cynoctonum crassifolium* (R. Br.) E. Mey., Comm. Pl. Afr. Austr. 216. 1838. *Cynanchum africanum* (L.) Hoffmanns. var. *crassifolium* (R. Br.) N. E. Br. in Dyer, Fl. Cap. 4(1): 749. 1908. *Cynoctonum crassiflorum* Krauss, Flora 27: 827. 1844 (spelling error for *C. crassifolium* R. Br.). TYPE: *collector unknown s.n.*, Herbarium Banks (BM). The fact that "*Cynanchum obtusifolium*, Linn. Suppl. 169?" is cited in synonymy does not render *Cynanchum crassifolium* R. Br. superfluous because the question mark is an expression of doubt (ICBN Art. 52.2, note 1, see Greuter et al., 1994).

Cynoctonum dregeanum Decne. in Candolle, Prodr. 8: 531. 1844. *Vincetoxicum dregeanum* (Decne.) Kuntze, Revis. Gen. Pl. 2: 424. 1891, nom. superfl. when published, substitute name for *Cynanchum crassifolium* R. Br.

Cynanchum pilosum R. Br., Mem. Wern. Nat. Hist. Soc. 1: 46. 1810. *Cynoctonum pilosum* (R. Br.) E. Mey., Comm. Pl. Afr. Austr.: 216. 1838. *Vincetoxicum pilosum* (R. Br.) G. Nicholson, Ill. Dict. Gard. 4: 160. 1887. *Cynoctonum crassifolium* E. Mey. var. *pilosum* (R. Br.) Decne. in Candolle, Prodr. 8: 530. 1844. *Cynanchum obtusifolium* var. *pilosum* (R. Br.) Schltr., Bot. Jahrb. Syst. 18, Beibl. 45: 10. 1894. nom. superfl. (cites *Periploca africana* L. in synonymy).

Cynanchum rotundifolium Thunb. ex Decne. in Candolle, Prodr. 8: 552. 1844. TYPE: not known. Pro. syn.

Cynanchum intermedium N. E. Br. in Dyer, Fl. Cap. 4(1): 747. 1908. TYPE: South Africa. Cape: prope Port Elizabeth, Oct. 1897, *West 1924* (holotype, SAM).

Plants twining, sparsely branched, 30–60 cm high, sarmentose with adventitious roots along the whole lower surface of the runner; subterranean organs rhizomatous in older plants, rhizome 5–10 mm diam. (e.g., *Bayliss 6144*, PRE). *Shoots* perennial, 50–100 cm long, 1–1.5 mm diam., herbaceous, glabrous or sparsely to densely covered with trichomes 0.5–0.6 mm long; in old plants basally woody with brownish bark. "*Stipules*" ovate, almost round, 4–6 mm long, 4–6 mm wide. *Leaves* with petioles 2–6 mm long, 2–3 colleters at the base of the leaves; leaf blades herbaceous to coriaceous, 20–30 mm long, 10–25 mm wide, ovate, basally cordate or rounded, apically mucronate, adaxially and abaxially glabrous, or isolatedly to sparsely covered with erect trichomes 0.4–0.5 mm long, evenly distributed over the whole surface. *Inflorescences* sciadioidal, 4–7-flowered, all flowers open at a time; peduncles 10–20 mm long, glabrous, or sparsely to densely covered with erect trichomes 0.5–0.6 mm long. *Flowers* sweetly scented; floral bracts 1.5–2.5 mm long, 0.5–0.7 mm wide at the base, triangular, glabrous, or with trichomes; pedicels 4–12 mm long, glabrous, or isolatedly to sparsely covered with erect trichomes 0.6–0.7 mm long. *Buds* 5–8 mm long, 1.5–2.5 mm diam., elongated-conical; aestivation basally imbricate, apically contorted. *Calyx* basally fused, abaxially with trichomes, lobes 2–2.7 mm long, 1–1.5 mm wide, triangular, apically acute. *Corolla* rotate, basally fused, 6–12 mm long, abaxially and adaxially purple to brown, glabrous (abaxially occasionally with a few trichomes); lobes 1.8–2.2 mm wide, recurved, oblong, apically acute, twisted. *Corona* white, tubular, 6–10 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, only Cs differentiated in shape. *Cs* without adaxial appendages; lobes of Cs flat, triangular to bifid (shallowly or more deeply, then giving the impression of a differentiated Ci), erect, with straight margins. *Gynostegium* 0.8–1.2 mm high, 1–1.5 mm diam., atop a stipe, 2–4 mm long. *Stamens* without free filaments, anthers deltoid, abaxially convex; anther wings 0.3–0.4 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.75–0.8 mm long, 0.45–0.5 mm wide, triangular, equaling the stamen in width, slightly inflexed. *Pollinarium*: corpusculum 0.2–0.25 mm long; caudicles 0.18–0.2 mm long, flattened, concavely recurved, triangular; pollinia apically attached to caudicles, 0.4–0.45 mm long, 0.15–0.18 mm wide, pyriform, elliptical in cross section. *Stylar head* 1–1.1 mm diam., 0.8–0.9 mm high; upper part 0.5–0.55 mm high, depressed-conical. *Follicles* usually one per flower, 45–60 mm long, 9–11 mm wide, obclavate, round in cross section, apically obtuse, medium brown, longitudinally slightly grooved; glabrous. *Seeds* 6–7 mm long, 3.3–3.7 mm wide, pyriform, light brown, seta and aseta side tuberculate, marginally with indistinct wing 1–1.1 mm wide with entire margin; coma 25–30 mm long. *Chromosome number*: $2n = 22$ (*Liede 2548, Liede & Meve 642*, MSUN).

Distribution and habitat. Africa: South Africa (Cape Province); 0–200 m, very rarely to 700 m; dunes, flats to gentle slopes, mostly on sand.

Comments. The late Onno Wijnands brought to my attention the fact that the lectotypification of this species (Linné 307.5, LINN) in Liede (1993) is invalid, because it is predated by his lectotypification (Wijnands, 1983).

Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

5. Cynanchum altiscandens K. Schumann, Abh. Königl. Akad. Wiss. Berlin 64. 1894. TYPE: Tanzania. Tanga: Usambara, Kwa Msfuza Hochwald, Aug. 1893, *Holst 9078* (holotype, B presumably destroyed; lectotype, designated here, K). Figure 7.

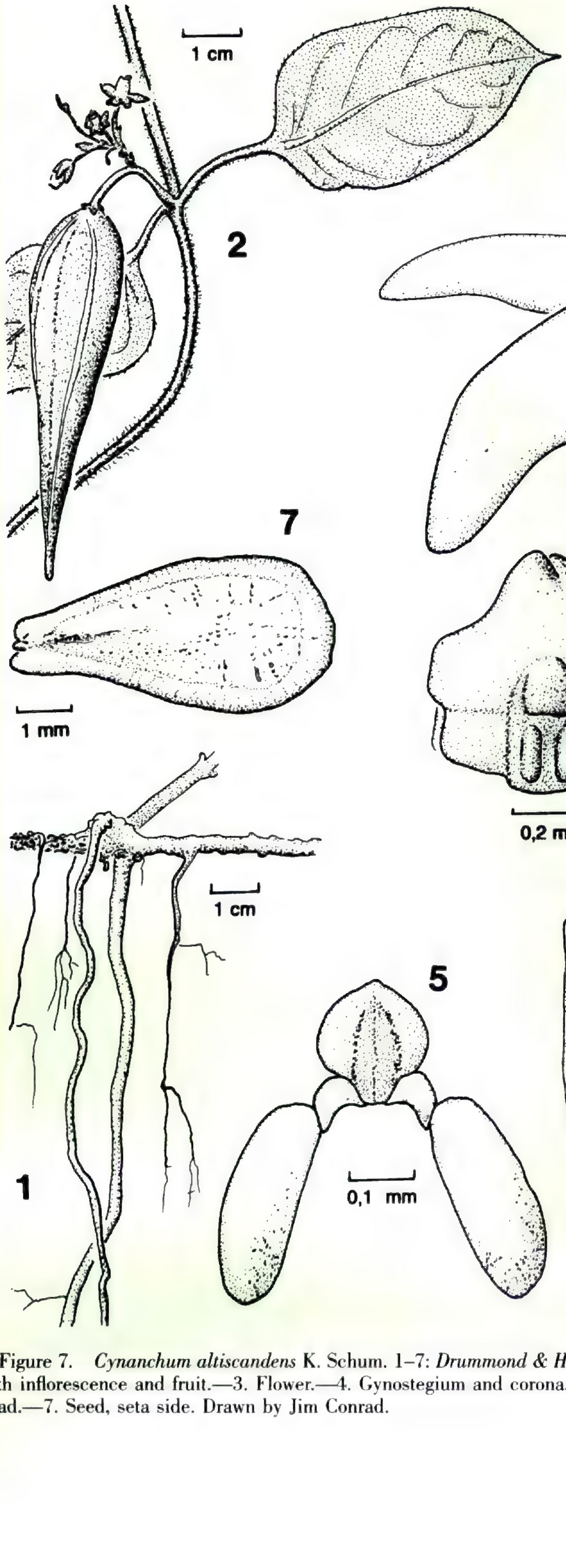


Figure 7. *Cynanchum altiscandens* K. Schum. 1–7: *Drummond & Hemsley 2106.*—1. Rhizome and roots.—2. Habit with inflorescence and fruit.—3. Flower.—4. Gynostegium and corona, partially removed.—5. Pollinarium.—6. Stylar head.—7. Seed, seta side. Drawn by Jim Conrad.

Cynanchum mensense Schweinf. ex K. Schum., Abh. Königl. Akad. Wiss. Berlin 64. 1894. TYPE: Eritrea: Gheleb, 1850 m, 17 Apr. 1891, *Schweinfurth 1505* (holotype, B presumably destroyed; lectotype, designated here, M).

Plants ascending, twining, 3–5 m high, richly and irregularly branched, sarmentose, with runners 2–3 mm diam., adventitious roots developing along the whole lower surface of the runner. *Shoots* herbaceous, glabrous to sparsely covered with flexuous trichomes 0.5–0.6 mm long; internodes 35–75 cm long, 1–1.5 mm diam. "*Stipules*" widely ovate, 8–12 mm long, 7–10 mm wide. *Leaves* with petioles 5–15 mm long, leaf blades herbaceous, 20–45 mm long, 12–28 mm wide, ovate, basally rounded with 1–3 colleters adaxially, apically acute or apically acuminate, apiculus 1–2 mm long, adaxially glabrous to sparsely covered with appressed trichomes 0.6–0.75 mm long, evenly distributed over the whole surface, abaxially glabrous or sparsely covered with appressed trichomes 0.5–0.6 mm long, concentrated on veins and margins. *Inflorescences* bostrychoid, 5–20-flowered, 5–12 flowers open at a time; rachis 1–5 mm long; peduncles 2–5 mm long, glabrous to densely covered with appressed trichomes 0.25–0.3 mm long. *Flowers* with floral bracts 0.6–1 mm long, 0.6–0.8 mm wide at the base, triangular, with trichomes; pedicels 5–8 mm long, glabrous to densely covered with flexuous trichomes 0.4–0.6 mm long. *Buds* 3–4 mm long, 1.5–2 mm diam., conical, with imbricate aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 1.2–1.6 mm long, 0.7–1 mm wide, ovate, apically acute. *Corolla* rotate, basally fused; 3.5–4.5 mm long, abaxially and adaxially yellowish green; lobes 0.8–1.2 mm wide, straight, patent, horizontal or declinate, oblong, apically acute. *Corona* white, tubular to urceolate, 3–3.5 mm high, exceeding the gynostegium, entirely obscuring it; C(is) consisting of Cs and Ci completely fused, only Ci differentiated. *Cs* not adnate to the filaments, without adaxial appendages. *Lobes of Ci* laminar, triangular (when flattened), producing a pronounced convex fold along the upper third of corona length, apically reflexed, with straight margins. *Gynostegium* 1.7–1.8 mm high, 1.8–2 mm diam., on a bulge of 0.4–1.3 mm length. *Stamens* without free filaments, anthers broader than high, trapezoidal, abaxially planar. Anther wings 0.6–0.65 mm long, convergent, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.8–0.9 mm long, 0.45–0.5 mm wide, triangular, narrower than the stamen, erect. *Pollinarium*: corpusculum 0.25–0.3 mm long, rhomboid; caudicles 0.15–0.2 mm long, flattened, straight, horizontal, trapezoidal; pollinia subapically attached to the caudicles, 0.35–0.4 mm long, 0.1–0.12 mm wide, ovoid to oblongoid, ovate in cross section. *Stylar head* 0.9–1 mm diam., 0.9–1 mm high; upper part 0.6–0.65 mm high, depressed-conical. *Follicles* one, occasionally two, per flower, pendulous, 55–65 mm long, 8–10 mm diam., obclavate, obtusely deltate in cross section, apically strongly beaked, keeled, medium brown, longitudinally grooved, glabrous or with isolated indumentum. *Seeds* 5–5.5 mm long, 2.2–2.5 mm wide, ovate, medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.4–0.6 mm wide wing with entire margin; coma 25–30 mm long. *Chromosome number*: $2n = 22$ (voucher: *Liede & Newton 2873*, ULM).

Distribution and habitat. Africa: Eritrea, Ethiopia (Harerge, Shewa, Sidamo), Kenya (K2, K3, K4, K6), Tanzania (T1, T2, T3), Uganda (U2, U3, U4, U7); 1000–2600 m; forest margins, thickets, roadside shrubbery. Widespread and frequent. Figure 8.

Flowering time. Almost all year, with peak between September and March.

Vernacular names. Sandab-Ngingichet (Kipsangali); Ngobito-Ol'dorobo, Sinande (Masai).

Uses. Browsed by all domestic stock; Wandorobo use stems to sew up the ends of bee hives.

Specimens seen. ERITREA. Oculè Cusai, Monte Metaten, 2500 m, 12 Sep. 1902, *Pappi 1483* (EA); Environs de Acrour, 1900 m, 8 Apr. 1892, *Schweinfurth & Riva 1692* (K). ETHIOPIA. **Harerge:** Harar, about 5 km on the rd. to Feddis, ca. 1800 m, 5 Dec. 1976, *Jansen & De Wit 7277* (WAG). **Shewa:** Mt. Zuquala, 2600 m, 7 Dec. 1961, *Meyer 7637* (K). **Sidamo:** 13 km S of Aghere Mariam on new rd., 1950 m, 9 May 1976, *Gilbert & Jefford 4316* (K). KENYA. **Central:** Kiambu, Kijabe, where stream cuts direct rd. to Kijabe across Kedong rift side through African Inland Mission, 1 Dec. 1963, *Verdcourt 3814* (B, K); Nyeri, Aberdares, near forest station, 13 Jan. 1922, *Fries 895* (K). **North Nyeri:** Nanyuki, Sweet Waters Ranch, 1750 m, 26 Dec. 1964, *Gillett 16569* (K); Masai, Narok, Orengitok ca. 12 mi. from Narok on rd. to Olokurto, 2530 m, 17 May 1961, *Glover, Gwynne & Samuel 1429* (K). **Rift Valley:** Nakuru, Nakuru National Park, 1740 m, 20 July 1975, *Gillett 20851* (K); Naivasha, Crater Lake, 1830 m, Nov. 1958, *Newbould 3634* (K); Trans Nzoia, Hoey's Bridge (Moi's Bridge), 1960 m, Sep. 1971, *Tweedie 4121* (K); Turkana, Mt. Lorosuk, Chemorongit Mtns., Karasuk, 2660 m, Aug. 1965, *Wilson 1644* (K). TANZANIA. **Arusha:** Mt. Meru, E slope, 1800 m, 12 Mar. 1968, *Greenway & Kanuri 13371* (K); Ngorongoro, 2330 m, 25 Nov. 1957, *Tanner 842* (K). **Mara:** Loliondo, 10 mi. W of Klein's Camp, ca. 2000 m, 11 Nov. 1953, *Tanner 1821* (K, MO); Moshi, Kilimanjaro Süd, 1650 m, 15 Jan. 1934, *Schlieben 4546* (K). **Tanga:** rd. to Lushoto town, 3 Mar. 1986, *Kisena 623* (K). UGANDA. Busoga, Usoga, Jan. 1894, *Scott Elliott 7227* (K); East Ankole, Mitooma, Lukiri, 1700 m, 11 Jan. 1989, *Rwaburindore 2752* (MO);

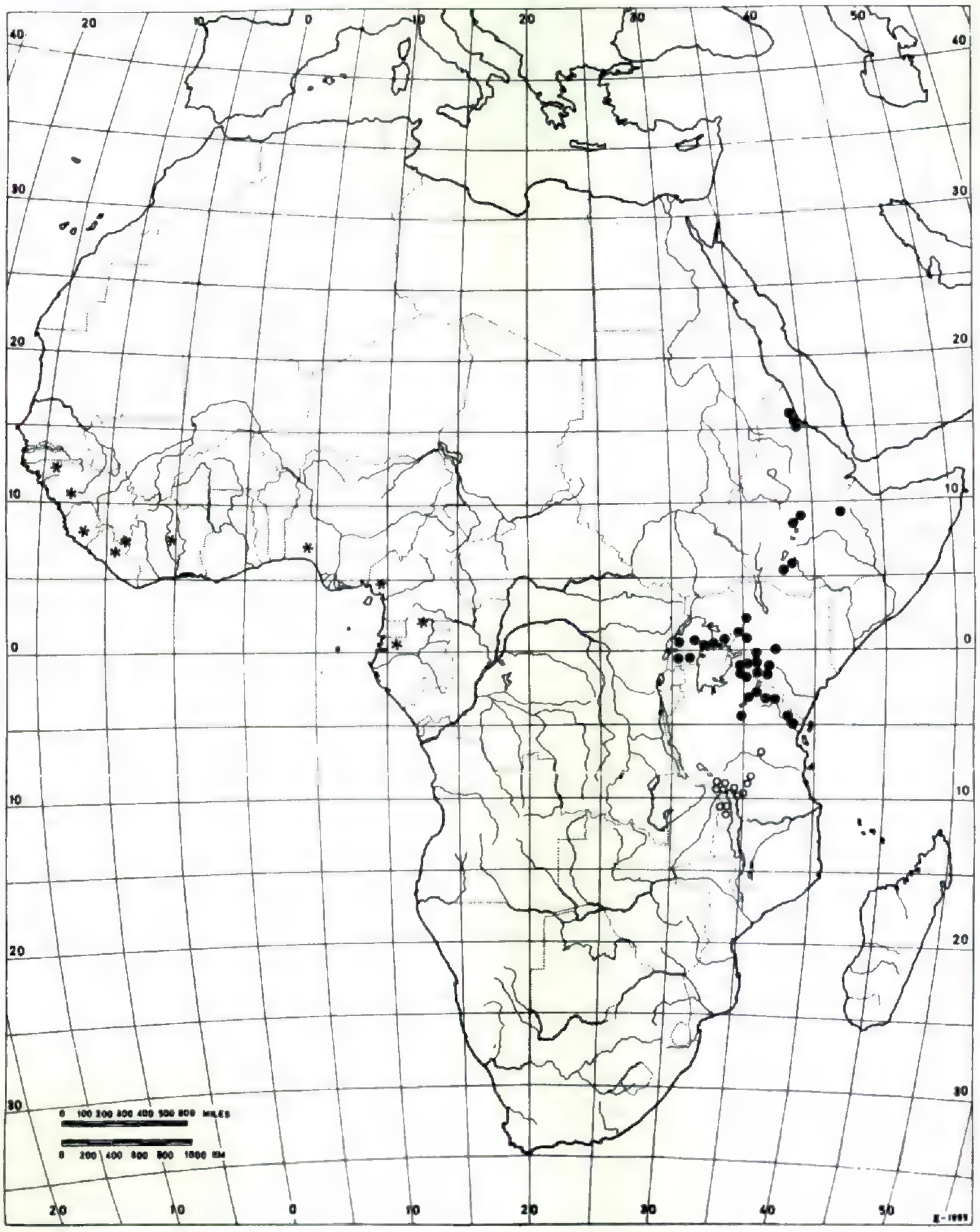


Figure 8. Known distribution of *Cynanchum altiscandens* (dots), *C. longipes* (asterisks), and *C. rungweense* (open circles).

Masaka, Kabula, 14 Mar. 1936, *Michelmore 1328* (K); Mengo, near Mukono, Nov. 1914, *Dümmer 1238* (BM, BOL); Mubende, Singo West, ½ mi. W of Kasanda trading center, 10 Aug. 1974, *Katende 2249* (K); Toro, N edge of Kihabule LFR, W of Katwe, Queen Elizabeth National Park, 1030 m, 22 Apr. 1969, *Lock 69/85* (EA).

Comments. *Cynanchum altiscandens* is closely related to *C. rungweense*, *C. ellipticum*, *C. natalitium*, *C. africanum*, and *C. zeyheri*, a group of species characterized by highly fused coronas and, with exception of *C. ellipticum*, stipitate gynostegia and the formation of runners or rhizomes just under the soil surface.

6. Cynanchum balense Liede, sp. nov. TYPE: Ethiopia. Bale: Rira, 3260 m, 20 Dec. 1959, *Mooney 8359* (holotype, K). Figure 9.

Cynanchum gonoloboides affinis cum foliis neuraphylis, fructibus incrassatis. Differt gynostegio sessili, partibus staminalibus interstaminalibusque coronae gynostegialis non nisi basaliter connatis; partibus staminalibus profunde bifidis.

Plants ascending, twining, 6–7 m high, richly and irregularly branched. *Shoots* perennial, herbaceous, isolatedly glabrescent with flexuous trichomes 0.4–0.5 mm long, basally woody with brownish bark; internodes 35–45 cm long, 3–3.5 mm diam. "*Stipules*" absent. *Leaves* with petioles 17–40 mm long; leaf blades coriaceous, 55–110 mm long, 35–60 mm wide, ovate, basally cordate with 9–11 colleters in the adaxial sinus; apically acuminate, apiculus 7–10 mm long, adaxially isolatedly covered with flexuous trichomes 0.4–0.45 mm long, evenly distributed over the whole surface, abaxially sparsely covered with flexuous trichomes 0.4–0.5 mm long, concentrated on veins and mar-

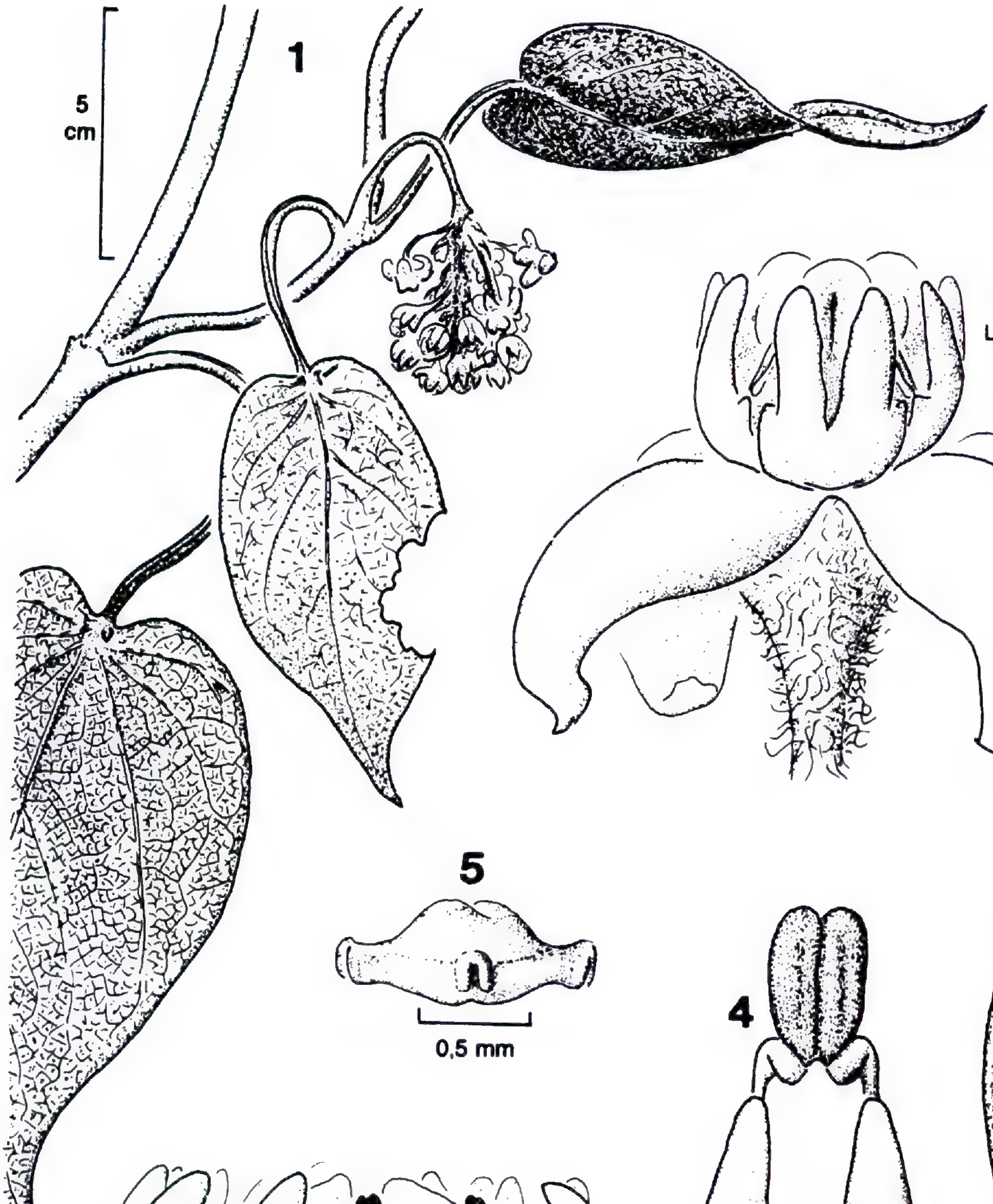


Figure 9. *Cynanchum balense* Liede. 1–6: *Mooney 8359*.—1. Habit with inflorescence.—2. Flower.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head.—6. Fruit. Drawn by Jim Conrad.

gins. *Inflorescences* basally dichasial, apically bostrychoid, 12–20-flowered, 5–15 flowers open at a time; rachis 20–50 mm long; peduncles 40–50 mm long, densely covered with flexuous trichomes 0.5–0.6 mm long. *Flowers* fragrant; floral bracts 5–6 mm long, 1–1.5 mm wide at the base, ovate, with trichomes; pedicels 15–20 mm long, densely covered with flexuous trichomes 0.5–0.6 mm long. *Buds* 4.5–5 mm long, 3.5–4 mm diam., ovoid, with imbricate aestivation. *Calyx* entirely free, abaxial surface with trichomes; lobes 4–4.2 mm long, 1.8–2 mm wide, ovate, apically acute to acuminate. *Corolla* rotate, basally fused; 4–5 mm long, abaxially and adaxially greenish purple; lobes 2–2.2 mm wide, straight, horizontal to declinate, oblong, apically acute to acuminate. *Corona* pink, 2.5–3 mm high, equaling the gynostegium in height, C(is) consisting of Cs and Ci only basally fused, only Cs differentiated. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, deeply bifid, apically erect, with straight, entire margins. *Gynostegium* 2–2.2 mm high, 1.4–1.6 mm diam., sessile. Anthers about as high as broad, trapezoidal, abaxially convex; anther wings 1.4–1.6 mm long, convergent, extending beyond the anther proper, consisting of distal and proximal ridge, with space between distal and proximal ridge papillose, proximal ridge curved; adjacent anther wings parallel, centrifugal. Connective appendages 0.7–0.8 mm long, 0.8–1 mm wide, ovate, equaling the stamen in width, strongly inflexed. *Pollinarium*: corpusculum 0.4–0.45 mm long, ovoid; caudicles ca. 0.15 mm long, cylindrical, concavely recurved; pollinia apically attached to the caudicles, 0.48–0.5 mm long, 0.15–0.17 mm wide, clavate. *Stylar head* 1.2–1.3 mm diam., 0.6–0.8 mm high; upper part 0.4 mm high, umbonate. *Follicles* one per flower, 90–95 mm long, 12–15 mm diam., obclavate, keeled, apically strongly beaked, medium brown, thick-walled, longitudinally grooved, glabrous. *Seeds* and *chromosome number* unknown.

Distribution and habitat. Africa: Ethiopia: Bale; 3260 m (at upper forest margin); patch of forest in pasture. Only known from the type collection. Probably rare and endangered, even though Rira is included in the Mt. Bale National Park (fide M. G. Gilbert). Figure 10.

Flowering time. December.

Comments. *Cynanchum balense* is a sister species of *C. gonoloboides*, with which it shares the characteristic dark green leaves with pronounced nervature as well as similar size and shape of the fruit.

7. Cynanchum blyttioides Liede, sp. nov. TYPE: Somalia. Sanaag, above Geei Harre, W of Gardo airstrip, 710–840 m, 7 Oct. 1980, *Beckett 428* (holotype, EA; isotype, K). Figure 11.

Fruticulus erectus, habitu *Blyttia* et *Diplostigma* similis, sed partibus staminalibus interstaminalibusque coronae gynostegialis late connatis, abaxialibus papillosis differt.

Plants erect, nontwining, 50–75 cm high, richly basicaulously branched. *Shoots* woody, with grayish bark, glabrous. "*Stipules*" absent. *Leaves* subsessile; leaf blades 3–4 mm long, 2–3 mm wide, ovate, basally rounded with 1–3 colleters adaxially, apically obtuse, marginally thickened, crenulate, adaxially and abaxially glabrous. *Inflorescences* sessile, sciadioidal, 2–4-flowered, all flowers open at a time. *Flowers* with floral bracts 0.8–1 mm long, 0.4–0.6 mm wide at the base, triangular, glandular over the whole surface; pedicels 2.5–3 mm long, glabrous. *Calyx* basally fused; lobes 1.2–1.3 mm long, 0.5–0.6 mm wide, triangular, apically acute. *Corolla* cyathiform, basally fused, with imbricate aestivation, 2–2.5 mm long; lobes 0.8–0.9 mm wide, incurved, triangular, apically acute. *Corona* cyathiform, abaxially papillose, 1.5–1.7 mm high, equaling the gynostegium in height; C(is) consisting of Cs and Ci fused for ¾ to ⅞ of total corona length, Cs and Ci differentiated, Ci longer than Cs (and about twice as broad; upper halves of Ci folded in over Cs), with straight margins. *Cs* not adnate to the filaments, appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, oblong, apically erect, with straight margins. *Lobes of Ci* laminar, ovate, producing a slight convex fold along the whole corona length, inflexed, with straight margins. *Gynostegium* 1–1.2 mm high, 0.9–1.1 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, hexagonal, abaxially biconcave; anther wings 0.65–0.7 mm long, parallel to each other, not extending along the whole length of the anther; the anther forming a "pseudostipe" 0.3–0.4 mm high, adjacent anther wings parallel, basally centrifugal, forming a distinct "mouth" with the basal lateral margin of the anther. Connective appendages 0.36–0.4 mm long, 0.5–0.55 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.15–0.17 mm long, margins of the corpuscular cleft basally widened; caudicles 0.09–0.1 mm long, flattened, convexly recurved, trapezoid; pollinia subapically attached to the caudicles, 0.2–0.25 mm long, 0.08–0.1 mm wide, ovoid. *Stylar head* 0.5–0.6 mm diam., 0.25–0.35 mm high; upper part 0.2–0.3 mm high, umbonate. *Follicles* one per flower,

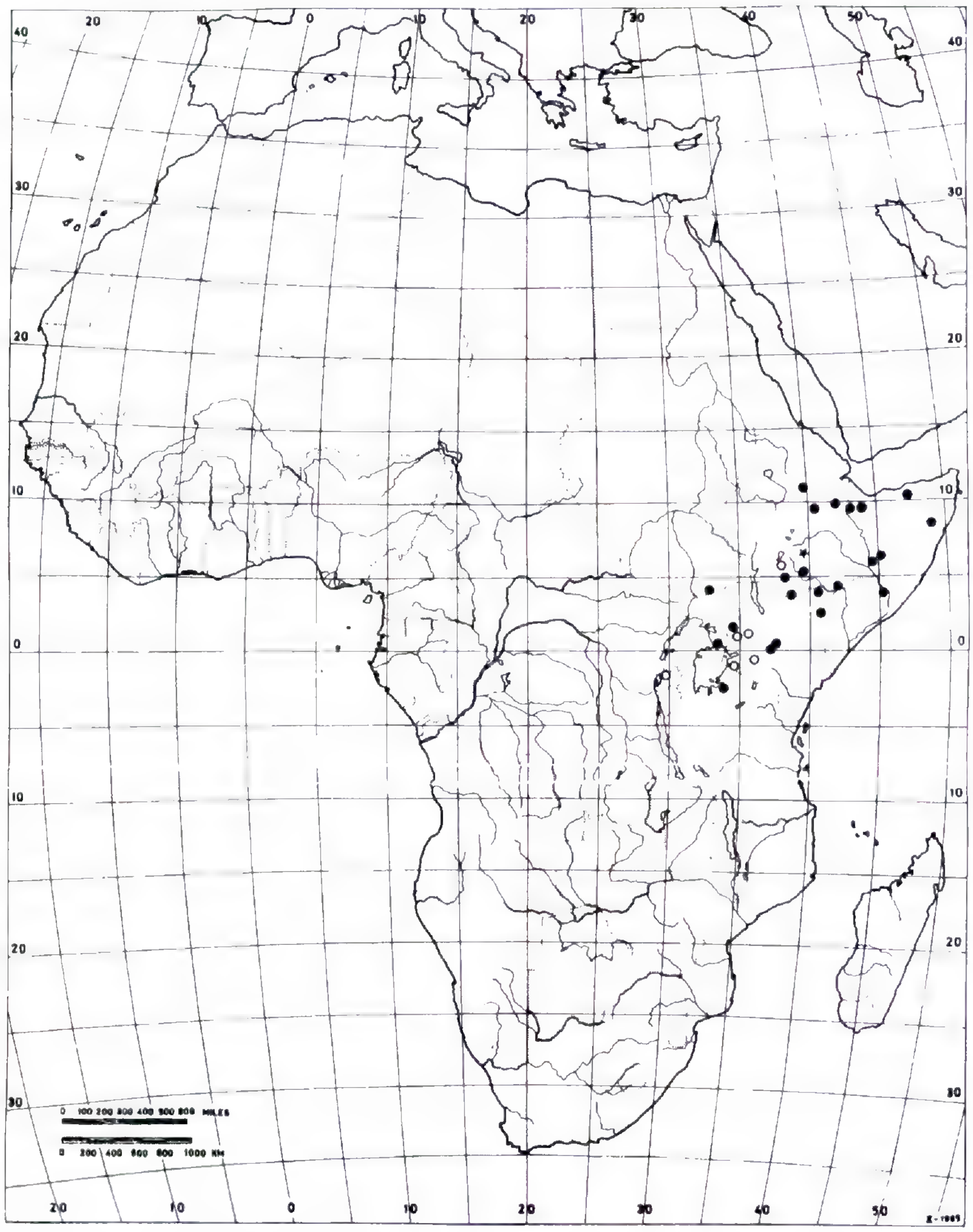


Figure 10. Known distribution of *C. balense* (star), *C. gonoloboides* (open circles), and *C. somaliense* (dots).

pendulous, 35 mm long, 7 mm diam., obclavate, obtusely triangular in cross section, apically strongly beaked, wingless, light brown, with reddish brown mottling, smooth, glabrous. *Seeds* 6–6.5 mm long, 3.5–4 mm wide, ovate, light brown, seta and aseta side densely covered with regularly arranged trichomes 0.5–0.7 mm long, marginally with wing 0.3–0.5 mm wide with entire margin; coma 12–15 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Somalia (Sanaag); 700–850 m; fragmented marine limestone hills, thin bush with poor grass cover. Rare and localized; but probably undercollected. Figure 12.

Flowering time. October.

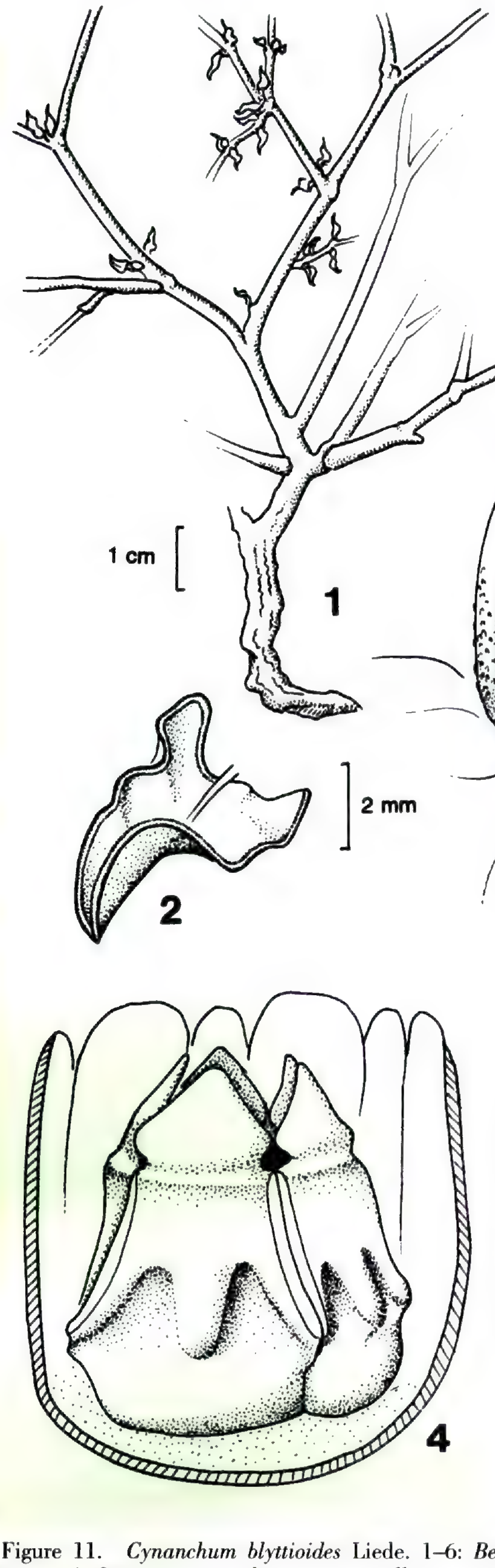
Vernacular name. Sod Keh.

Uses. Fruits edible, nutty flavor; fruit and latex medicinal.

Comments. The affinities of *Cynanchum blyttioides* are unclear. In habit, it resembles strongly the genus *Blyttia,* though corona structure places it in *Cynanchum.* Within *Cynanchum,* it resembles the two other new Somalian species, *C. crassiantherae* and *C. rubricoronae,* in habit and the peculiar undulated leaves. The slightly papillose corona reminds one of *C. clavidens.*

The specimen in EA has been chosen as holotype because the K specimen is rather poor.

7a. Cynanchum clavidens N. E. Br. subsp. **clavidens,** Bull. Misc. Inform., Kew 106: 256. 1895. *Cynanchum flavidens* N. E. Br., Index Kewensis Suppl. 1: 121. 1906. spelling error for *Cynanchum clavidens.* TYPE: Somalia. Boobi, 5 Feb. 1933, *James & Thrupp s.n.* (holotype, K). Figure 13.



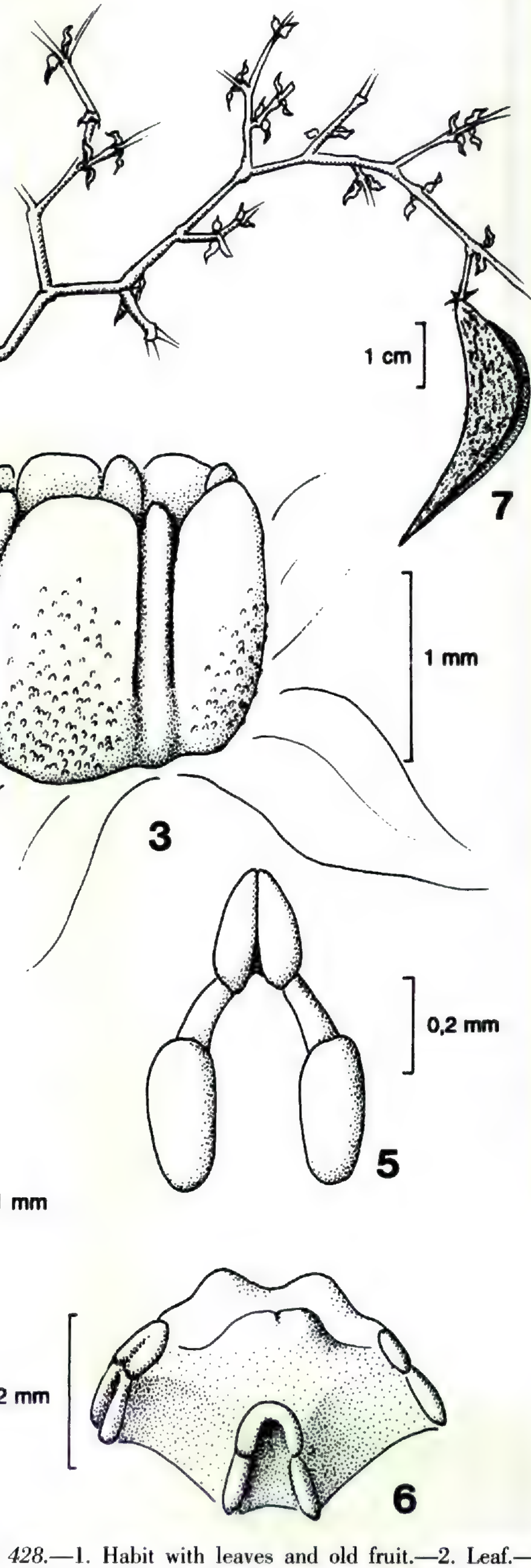


Figure 11. *Cynanchum blyttioides* Liede. 1–6: *Beckett 428.*—1. Habit with leaves and old fruit.—2. Leaf.—3. Flower.—4. Gynostegium and corona, partially removed.—5. Pollinarium.—6. Stylar head. Drawn by G. Hintze.

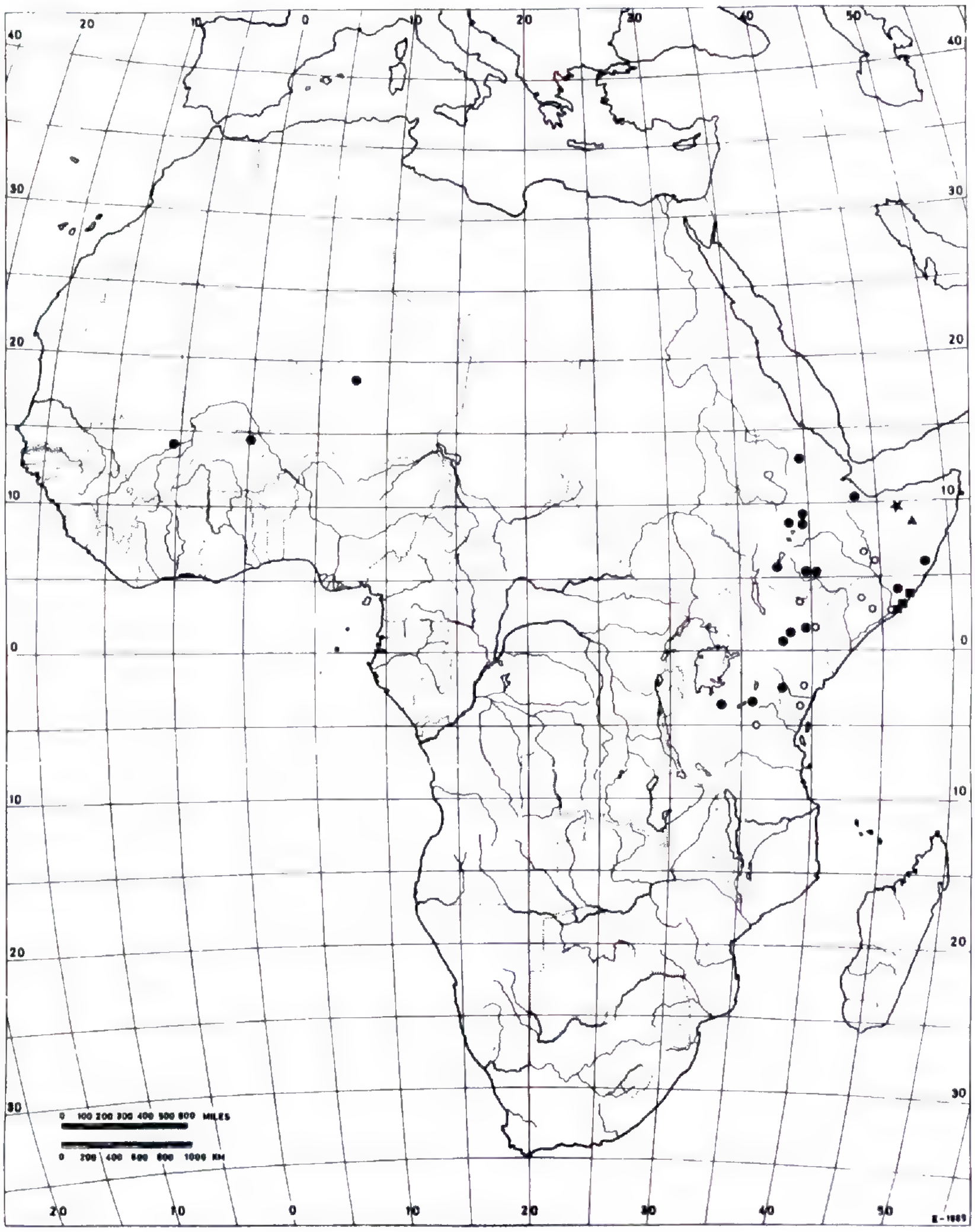


Figure 12. Known distribution of *C. blyttioides* (star), *Cynanchum clavidens* subsp. *clavidens* (open circles), subspecies *hastifolium* (dots), *C. crassiantherae* (squares), and *C. rubricoronae* (triangle).

Plants ascending to erect, twining, 1–2.5 m high; irregularly branched. *Shoots* probably deciduous (*O'Brien 43*), apically herbaceous, glabrescent to sparsely covered with flexuous trichomes 0.3–0.35 mm long, along a single line; basally woody, with yellowish to brownish bark; internodes 1–5.5 cm long, 1.5–2 mm diam. "*Stipules*" hastate, 7–10 mm long, 6–8 mm wide, apically obtuse. *Leaves* with petioles 6–14 mm long; leaf blades herbaceous, 10–75 mm long, 4–35 mm wide, hastate, basally cordate to lobate, lobes 4–7 mm long, with 1–2 colleters in the adaxial sinus, apically acute to acuminate, adaxially isolatedly to sparsely covered with flexuous trichomes 0.3–0.4 mm long, concentrated on veins and margins, abaxially papillose, glabrous to isolatedly covered with flexuous trichomes 0.3–0.4 mm long, concentrated on veins and margins. *Inflorescences* sciadioidal, sessile, 3–6-flowered, all flowers open at a time. *Flowers* with floral bracts 1–1.5 mm long, 0.4–0.7 mm wide at the base, triangular, glabrous; pedicels 3–10 mm long, sparsely to densely covered with flexuous trichomes 0.4–0.5 mm long, along a single line. *Buds* (3.5–)6–6.5 mm long, 1.5–2 mm diam., elongated-conical to conical, with imbricate, apically contorted aestivation. *Calyx* basally fused, abaxial surface with trichomes; lobes 1.6–2 mm long, 0.7–1 mm wide, linear to triangular or ovate, apically acute. *Corolla* rotate, basally fused; (3–)5–6.5 mm long, abaxially creamish green, adaxially green; lobes 1–1.2 mm wide, decurved, lanceolate, apically obtuse, with revolute margins. *Corona* tubular, white, abaxially apically papillose, 2–3 mm high, equaling to exceeding the gynostegium in height (except for the appendage of the stylar head), but not obscuring it; C(is) consisting of Cs and Ci fused for about ¾ of

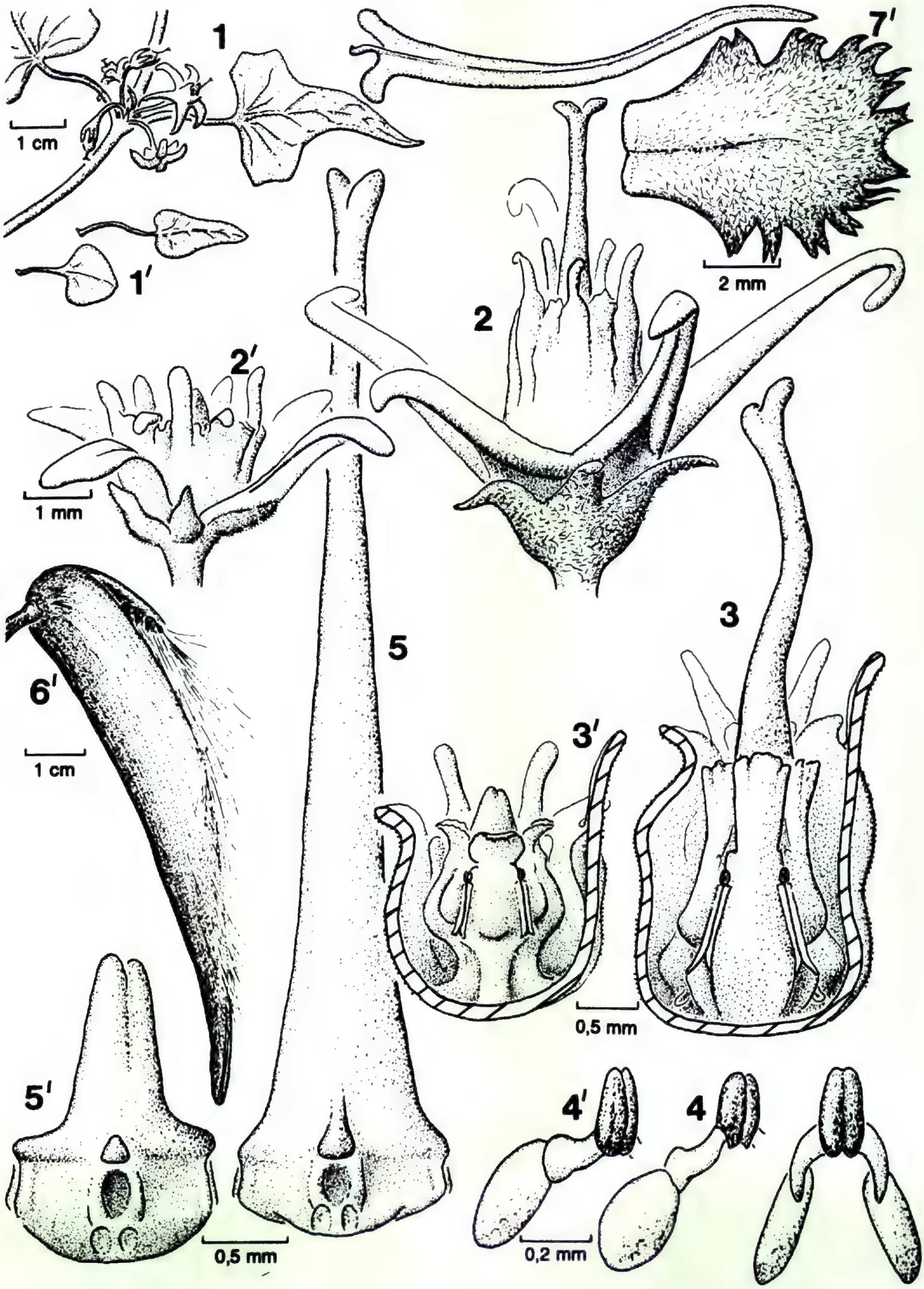


Figure 13. *Cynanchum clavidens* N. E. Br. 1–5: subspecies *clavidens*. 1′–7′: subspecies *hastifolium* (N. E. Br.) Liede.—1. Node with inflorescence (*O'Brien 43*), deviating leaf shape (*Hucks 272*).—1′. Leaf shapes; left: *Gillett 13863*, right: *Gilbert et al. 7399*.—2, 2′. Flower.—3, 3′. Gynostegium and corona (partially removed).—4, 4′. Pollinarium.—5, 5′. Stylar head. 2–5: *Liede & Newton 3160*. 2′–5′: *Gillett 13863*. 6′, 7′: *Gilbert et al. 7399*.—6′. Fruit.—7′. Seed, seta side. Drawn by Jim Conrad.

total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, not appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, ovate, producing a pronounced convex fold, apically erect. *Lobes of Ci* laminar, ovate to oblong, erect to reflexed, with laterally involute margins. *Gynostegium* 1.4–1.7 mm high (without appendage of stylar head), 1–1.2 mm diam., sessile. *Stamens* with free filaments 0.7–0.8 mm long; anthers about as high as broad, trapezoidal, abaxially planar to convex; anther wings 0.8–0.85 mm long, convergent, extending along the whole length of the anther, adjacent anther wings parallel, centrifugal, basally forming a distinct "mouth" with the basal lateral margin of the anther. Connective appendages 0.6–0.7 mm long, 0.5–0.6 mm wide, ovate, equaling the stamen in width, erect, with denticulate margins. *Pollinarium*: corpusculum 0.3–0.35 mm long; caudicles 0.35–0.4 mm long, cylindrical, s-shaped, convex-concave; pollinia subapically attached to the caudicles, 0.35–0.4 mm long, 0.1–0.12 mm wide, ovoid, ovate in cross section. *Stylar head* white, 0.6–0.65 mm diam., 1–2.5 mm high; upper part 0.7–2.2 mm high, obinfundibuliform (the appendage exceeding the corona is the main diagnostic feature of the subspecies). *Follicles* normally one per flower, pendulous, 100–120 mm long, 15–20 mm diam., obclavate, round in cross section, apically strongly beaked, green with dark brown mottling, longitudinally grooved, glabrous. *Seeds* ca. 7.5 mm long, 4.5 mm wide, ovate, medium brown, seta and aseta side papillose with regularly arranged papillae, and with sparse, regularly arranged trichomes 0.15–0.25 mm long, marginally with wing 0.6–0.8 mm wide, with denticulate margin; coma 25–30 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Ethiopia (Bale, Harerge), Kenya (K1, K4, K7), Somalia (Bakool, Bay, Shabeellaha Dhexe), Tanzania (T5); 230–1400 m; dry savanna, *Acacia–Commiphora* bushland. Widespread, but localized. Figure 12.

Flowering time. January to July.

Use. Fruits edible.

Selected specimens examined. ETHIOPIA. **Harerge:** Mt. Scillavel Park, Tira R. area, 8 Apr. 1956, *Scimono 88* (K). KENYA. **Central:** Kitui, Tsavo East National Park, Tira R. area, 450 m, Apr. 1965, *Hucks 272* (K). **Coast:** Kwale, Mackinnon Rd., Tara desert, 400 m, Oct. 1965, *Tweedie 3199* (K). **Northern Frontier:** Moyale, 10 km from Moyale barrier, 10 Dec. 1993, *Liede & Newton 3160* (ULM). SOMALIA. Bakool, Wajid (17 km E of Uegit on rd. to Oddur), 415 m, 22 May 1983, *Gillett & Hemming 24352* (K); Bay, Bur Heybe, 230–375 m, 28 Apr. 1985, *O'Brien 43* (K); Shabeellaha Dhexe, Johwar, SW Morajiiddo, ca. 4–6 km S Bulo Caano, 17 July 1988, *Kilian & Lobin 1762* (K). TANZANIA. **Dodoma:** between Mando and Goma, 12 mi. E of Kondoa, 1400 m, 20 Jan. 1962, *Polhill & Paulo 1239* (K).

7b. Cynanchum clavidens N. E. Br. subsp. **hastifolium** (N. E. Br.) Liede, comb. nov. Basionym: *Cynanchum hastifolium* N. E. Br., Bull. Misc. Inf., Kew 1895: 257. Oct. 1895. TYPE: Ethiopia. Tigray: near Djeladjeranne, 29 Aug. 1840, *Schimper 1690* (holotype, K; isotype, P). Figure 13.

Cynanchum hastifolium K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 253. Oct. 1895. TYPE not located (see comments).

Plants ascending, twining, 0.5–1 m high, sparsely and irregularly branched. *Shoots* basally woody, with yellowish brown bark, apically herbaceous, glabrescent to sparsely covered with flexuous trichomes 0.3–0.35 mm long, along a single line; internodes 1.5–4.5 cm long. "*Stipules*" hastate, 7–10 mm long, 6–8 mm wide, apically obtuse. *Leaves* with petioles 6–25 mm long; leaf blades herbaceous, 12–48 mm long, 8–25 mm wide, hastate, basally truncate to cordate with 2–3 colleters in the adaxial sinus, apically acute, adaxially isolatedly covered with flexuous trichomes 0.5–0.6 mm long, evenly distributed over the whole surface, abaxially papillose, glabrous to isolatedly covered with flexuous trichomes 0.5–0.6 mm long, restricted to veins and margins. *Inflorescences* sciadioidal, sessile, 5–16-flowered, all flowers open at a time. *Flowers* with floral bracts 0.8–1 mm long, 0.5–0.6 mm wide at the base, ovate; pedicels 6–8 mm long, densely covered with flexuous trichomes 0.3–0.4 mm long. *Buds* 3–4 mm long, 1.2–1.8 mm diam., conical, with imbricate, apically contorted aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 2–3 mm long, 0.4–0.6 mm wide, linear to lanceolate, apically acute. *Corolla* rotate, basally fused; 4–5 mm long, abaxially and adaxially green; lobes 0.8–1 mm wide, horizontal to decurved, linear to lanceolate, apically acute, with revolute margins. *Corona* white, tubular to urceolate, abaxially apically papillose, 5.5–6 mm high, exceeding the gynostegium (including stylar head) and partly obscuring it; C(is) consisting of Cs and Ci fused for about ⅔ of total corona length, Cs and Ci differentiated, Ci shorter than to as long as Cs. *Cs* not adnate to the filaments, not appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar to filamentous, ovate-oblong, producing a pronounced convex fold. *Lobes of Ci* laminar,

very elongatedly oblong, producing a pronounced convex fold along the upper two-thirds of corona length, erect, with laterally involute margins. *Gynostegium* 4–4.2 mm high, 2.3–2.5 mm diam., sessile. *Stamens* with free filaments 0.8–0.9 mm long; anthers about as high as broad, trapezoidal, abaxially planar; anther wings 0.45–0.5 mm long, convergent, extending along the whole length of the anther, adjacent anther wings parallel, centrifugal, basally forming a distinct "mouth." Connective appendages 0.85–0.9 mm long, 0.85–0.9 mm wide, ovate, broader than the stamen, erect, with denticulate margins. *Pollinarium*: corpusculum 0.26–0.28 mm long; caudicles 0.2–0.23 mm long, flattened, s-shaped, convex-concave, trapezoid; pollinia subapically attached to the caudicles, 0.4–0.42 mm long, 0.2–0.22 mm wide, ovoid, ovate in cross section. *Stylar head* white, 1.2–1.3 mm diam., 1.4–1.5 mm high; upper part 1–1.2 mm high, umbonate (only in *Gillett et al. 22615*) or elongated-conical (not exceeding the corona, in contrast to subsp. *clavidens*). *Follicles* normally one per flower, pendulous, 60–100 mm long, 10–15 mm diam., obclavate, round in cross section, apically strongly beaked, light to medium brown, longitudinally grooved, glabrous. *Seeds* 6.5–7.5 mm long, 4–4.5 mm wide, ovate, medium brown, seta and aseta side papillose with regularly arranged papillae, and with sparse, regularly arranged trichomes 0.15–0.25 mm long, marginally with wing 0.6–0.8 mm wide, with denticulate margin; coma 22–25 mm long. *Chromosome number*: $2n = 22$ (voucher: *Liede & Newton 3226*, ULM).

Distribution and habitat. Africa: Eritrea, Ethiopia (Gamo Gofa, Shewa, Sidamo, Tigray), Kenya (K1, K4), Mali, Niger, Somalia (Hiiraan, Mudug, Sanaag), Tanzania (T1, T2), Upper Volta; 200–1600 m; *Acacia seyal–Balanites* bushland. Widespread, but localized. Figure 12.

Flowering time. March to October.

Vernacular name. Gesuriat (Somali); Shubkax (Hobyo).

Uses. Fruits edible.

Selected specimens examined. ERITREA. E of Amba-Tokhan, 27 Feb. 1892, *Schweinfurth & Riva 398m* (FT, K). ETHIOPIA. **Gamo Gofa:** Gidole area, Argoba, 1400 m, 16 Apr. 1985, *Haugen 576* (K). **Shewa:** 1 km W of Birrta on track to Koye; 10 km N of Meki, 1700 m, 22 Sep. 1973, *Gilbert & Gelahun Abate 3123* (K). **Sidamo:** Borana, 46 mi. SE of Neghelle on road to Filtu and Dolo, 1450 m, 16 Apr. 1974, *Ash 2421* (K, MO, UPS). **Tigray:** 37 km S of Quiha, along the road to Maichew, ca. 2150 m, 5 Sep. 1970, *De Wilde 6986* (MO, WAG). KENYA. **Central:** Machakos, Ithaba, 1000 m, 15 May 1938, *Bally 8357* (K). **Northern Frontier:** 13 km N of Isiolo on rd. to Marsabit, 1050 m, 2 Nov. 1978, *Gilbert, Gathachi & Gatheri 5316* (K). NIGER. Plateau Koutou, 9 Sep. 1966, *Fabrègues 2065* (P). SOMALIA. Hiiraan, 5 km W of Mukwakori on the rd. to Buloburti, 200 m, 13 June 1979, *Gillett, Hemming & Watson 22615* (K); Mudug, 53.4 km N of Hobyo along Hoby-Budbud inland route, 26 May 1987, *Wieland 4319* (MO); Sanaag, Dobo pass, 1330 m, 5 Feb. 1933, *Gillett 4952* (FT, K). TANZANIA. **Arusha:** Mbulu, Mbagaya River–Ndabash, Lake Manyara Nat. Park, 1580 m, 2 Mar. 1964, *Greenway & Kanuri 11282* (K). **Shinyanga:** Shinyanga, *Koritschoner 2084* (K). UPPER VOLTA. Markoye, 21 Aug. 1975, *Toutain 46782* (P).

Comments. Both *Cynanchum hastifolium* N. E. Br. and *C. hastifolium* K. Schum. were described in October 1895, so that priority cannot be established. Here, the common practice to attribute the name to N. E. Brown, who provided a detailed description and a type, is followed. Schumann, in contrast, just mentioned the taxon and did not indicate any type material.

Cynanchum macinense A. Chev. [Explor. Bot. Afrique Occ. Franç. 1: 435. 1920, nomen nudum. Mali. Macina, pays de Habés, de Koboro-Kendé à Kanikombolé, 2 Sep. 1910, *Chevalier 24861* (P)] represents this taxon.

The differences between subspecies *hastifolium* and subspecies *clavidens* are of such minor nature that species rank cannot be maintained. The best distinguishing character is the long-exserted stylar head in subspecies *clavidens*. Mature buds and flowers of subspecies *clavidens* are almost always much larger than those of subspecies *hastifolium*, but floral size is quite variable in both subspecies. Subspecies *clavidens* commonly inhabits low-lying, eastern localities; subspecies *hastifolium* is commonly found in the more western highlands. This pattern, however, breaks down in southern Somalia, where subspecies *hastifolium* is found in low-lying coastal areas. The distribution of subspecies *hastifolium* is remarkable for the fact that it is one of the very few African species that shows a marked disjunction between East and West Africa.

Cynanchum clavidens shows affinities to the two Somalian endemics, *C. crassiantherae* and *C. rubricoronae*, but is otherwise isolated in *Cynanchum*.

The only known material of *Perianthostelma* Baillon, a specimen with the unpublished name P. abyssinicum in P, represents *C. clavidens* subsp. *hastifolium*.

8. Cynanchum crassiantherae Liede, sp. nov. TYPE: Somalia. Shaabeellaha Dhexe, 10–12 km N of Adale on rd. to Haji Ali, 15 m, May–June 1983, *Gillett & Hemming 24513* (holotype, K; isotype, EA). Figure 14.

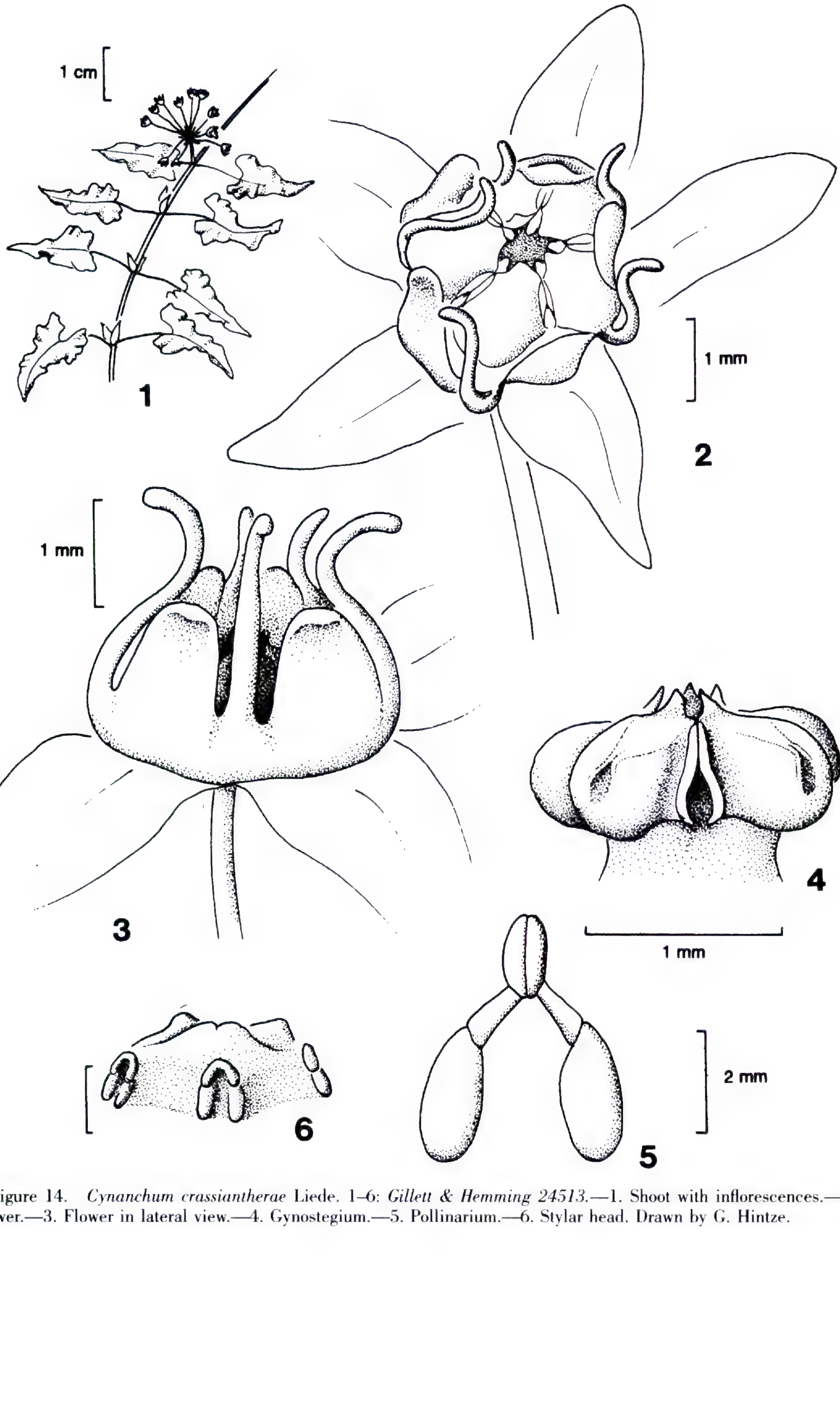


Figure 14. *Cynanchum crassiantherae* Liede. 1–6: *Gillett & Hemming 24513*.—1. Shoot with inflorescences.—2. Flower.—3. Flower in lateral view.—4. Gynostegium.—5. Pollinarium.—6. Stylar head. Drawn by G. Hintze.

Plantae erectae, rhizomatosae, foliis carnosulis, marginale crenulatibus; partibus staminalibus interstaminalibusque coronae gynostegialis ad mediam connatis; partibus staminalibus filamentosibus apicale reflexis; gynostegio breve stipitato, antheris crassis.

Plants erect, 20–25 cm high, sparsely basicaulously branched; rhizomatous, rhizomes 2–2.5 mm diam. *Shoots* herbaceous, glabrous; internodes 12–20 cm long, 1–1.5 mm diam. "*Stipules*" ovate, 3–8 mm long, 2–3.5 mm wide. *Leaves* with petioles 10–15 mm long; leaf blades fleshy, 15–25 mm long, 10–13 mm wide, triangular, basally lobate to auriculate, lobes 3–5 mm long, without colleters, apically acute to acuminate, adaxially and abaxially glabrous, margins thickened, crenulate. *Inflorescences* bostrychoid to sciadioidal, 10–16-flowered, 8–12 flowers open at a time. *Peduncles* 0–2 mm long, glabrous. *Flowers* with floral bracts 2–2.2 mm long, 0.2–0.3 mm wide at the base, linear, glabrous; pedicels 5–8 mm long, glabrous. *Buds* 2.8–3 mm long, 1.8–2 mm diam., conical, with imbricate aestivation. *Calyx* basally fused, abaxial surface glabrous; lobes 1.6–1.8 mm long, 0.4–0.5 mm wide, ovate-lanceolate, apically acute. *Corolla* rotate, basally fused; 3–3.5 mm long, abaxially and adaxially yellowish green; lobes 1–1.2 mm wide, horizontally spreading, oblong, apically acute. *Corona* cyathiform, white, 1.8–2 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci fused for about ⅓ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs lobes filamentous, apically reflexed. *Lobes of Ci* laminar, ovate to triangular, flat, erect. *Gynostegium* 1–1.1 mm high, 1.6–1.7 mm diam., atop a stipe, 0.4–0.5 mm long. *Stamens* without free filaments; anthers about as high as broad, massive, deltoid, abaxially convex; anther wings 0.4–0.45 mm long, parallel to each other, extending along the whole length of the anther, with space between distal and proximal ridge of anther wings glabrous; adjacent anther wings divergent toward the base, in the same plane as the anther. Connective appendages 0.5–0.6 mm long, 0.4–0.5 mm wide, triangular, equaling the stamen in width, slightly inflexed. *Pollinarium*: corpusculum 0.2 mm long, ovoid; caudicles 0.1 mm long, flattened, straight, declinate, triangular; pollinia subapically attached to the caudicles, 0.3–0.35 mm long, 0.1–0.12 mm wide, ovate in cross section, oblongoid. *Stylar head* 0.7–0.8 mm diam., 0.6–0.65 mm high; upper part 0.3 mm high, equaling the lower part in height, conical. *Fruits, seeds,* and *chromosome number* unknown.

Distribution and habitat. Africa: Somalia (Galguduud, Shabeellaha Dhexe); < 50 m; coastal dunes. Rarely collected. Figure 12.

Flowering time. May.

Additional specimens examined. SOMALIA. Galguduud, 21 km on rd. between Ceeldheer (El Dere) and Cadale, 40 m, 30 May 1989, *Thulin & Abdi M. Dahir 6718* (K); Shabeellaha Dhexe, 13 km N of Cadale along rd. to Ceeldheer, 10 m, 6 May 1990, *Thulin, Hedrén & Abdi M. Dahir 7231* (UPS).

Comments. *Cynanchum crassiantherae* is closely related to another Somali endemic, *C. rubricoronae.* It is clearly distinct from this and all other species of *Cynanchum* by its massive anthers.

9. Cynanchum ellipticum (Harvey) R. A. Dyer, Mem. Bot. Surv. South Africa 17: 138. 1937. *Bunburia elliptica* Harvey, Gen. S. Afr. Pl. 416. 1838. TYPE: South Africa. Cape: near Grahamstown, *Bunbury s.n.* (holotype, Herb. Hook. 1867, K).

Plants twining, 1.5–3 m high, richly branched; subterranean organs consisting only of fibrous roots. *Shoots* perennial, 200–300 cm long, 1–1.5 mm diam., herbaceous, glabrous, basally woody with grayish bark. "*Stipules*" ovate, almost round, 4–6 mm long, 4–6 mm wide. *Leaves* with petioles 5–15 mm long; leaf blades herbaceous, 20–40 mm long, 10–20 mm wide, elliptic to oblong, basally rounded with 2 colleters adaxially, apically obtuse to acute, apiculate, adaxially and abaxially glabrous. *Inflorescences* bostrychoid to sciadioidal, 2–15(rarely –30)-flowered, 4–10 flowers open at a time; rachis to 8 mm long; peduncles 12–20 mm long, glabrous. *Flowers* sweetly scented; floral bracts 0.8–1 mm long, 0.5–0.7 mm wide at the base, triangular, glabrous; pedicels 5–10 mm long, glabrous. *Buds* 2.5–3.5 mm long, 1.5–2.5 mm diam., ovoid; aestivation imbricate. *Calyx* basally fused, abaxially glabrous; lobes 0.8–1.2 mm long, 0.4–0.6 mm wide, ovate to oblong, apically obtuse. *Corolla* rotate, basally fused, spreading to recurved, 2.5–4 mm long, abaxially and adaxially glabrous, brown to green; lobes 0.8–1.2 mm wide, spreading to recurved, cucullate, apically obtuse, straight, or apically twisted. *Corona* white, cyathiform, 2.5–3.5 mm high, exceeding the gynostegium but not obscuring it, abaxially glabrous; C(is) consisting of Cs and Ci completely fused; upper margin entire or irregularly crenulate. *Cs* without adaxial appendages. *Gynostegium* 1–1.4 mm high, 1.2–1.6 mm diam., sessile. *Stamens* without free filaments, anthers broader than high, trapezoidal, abaxially convex; anther wings 0.5–0.6 mm long, convergent, extending beyond the anther proper forming a basal arch, adjacent anther wings

parallel, in the same plane as the anther. Connective appendages 0.35–0.4 mm long, 0.25–0.3 mm wide, triangular, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.2–0.22 mm long; caudicles 0.15–0.17 mm long, flattened, straight, declinate, thickened at the insertion of the pollinium, trapezoid; pollinia laterally attached to the caudicles, 0.3–0.35 mm long, 0.1–0.12 mm wide, ovate, round in cross section. *Stylar head* 0.8–0.85 mm diam., 0.7–0.8 mm high; upper part 0.45–0.48 mm high, depressed-conical. *Follicles* 45–60 mm long, 6–8 mm wide, obclavate, obtusely deltate in cross section, apically strongly beaked, keeled, medium brown, longitudinally slightly grooved, glabrous. *Seeds* 6–7 mm long, 3.5–4.5 mm wide, pyriform, dark brown, seta and aseta side tuberculate and sculptured with longitudinal ridges (less pronouncedly so on the aseta side); margins wingless, entire; coma 25 mm long. *Chromosome number*: $2n = 22$ (voucher: *Liede 2933*, ULM).

Distribution and habitat. Africa: Mozambique, South Africa (Cape Province, Natal, Transvaal); 0–1300 m; flats to moderate slopes, in sand or between rocks, indigenous forests and forest margins, thickets, frequently in disturbed habitats.

Comments. In Liede (1993), this species was discussed under *C. capense* Thunb. However, *Cynanchum capense* L.f. [Suppl.: 168. 1782] was interpreted by N. E. Brown (1908) as a synonym of *Pentatropis microphylla* Wight & Arn., because the description is clearly taken from the specimen *König s.n.*, which represents *Pentatropis microphylla*. The other specimen cited in the protologue (*Sparrmann s.n.*) represents *Cynanchum obtusifolium* L.f. *Cynanchum capense* Thunb. [Prodr. Fl. Cap.: 47. 1800; type: *Thunberg s.n.* , UPS 6289, UPS] represents a later homonym of *Cynanchum capense* L.f.

Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993) under *C. capense*.

10. Cynanchum falcatum Hutchinson & E. A. Bruce, Bull. Misc. Inform., Kew 1941: 145. 1941. TYPE: Somalia. Woqooyi Galbeed, boundary, 44°10′E, 8°57′N, 1290 m, 4 Oct. 1932, *Gillett 4114* (holotype, K). Figure 15.

Plants ascending, twining, 1–1.5 m high, richly and irregularly branched. *Shoots* herbaceous, sparsely to densely covered with appressed trichomes 0.3–0.4 mm long; internodes 3–8 cm long, 0.5–1 mm diam. "*Stipules*" absent. *Leaves* with petioles 2–10 mm long; leaf blades herbaceous, 20–40 mm long, 2–16 mm wide, triangular to falcate, basally truncate, obtuse, rounded or cordate with 4–5 colleters in the adaxial sinus, apically acute to acuminate, adaxially papillose, sparsely covered with erect trichomes 0.3–0.4 mm long, evenly distributed over the whole surface, abaxially sparsely to densely covered with appressed trichomes 0.23–0.3 mm long, evenly distributed over the whole surface. *Inflorescences* bostrychoid to sciadioidal, 5–12-flowered, 4–10 flowers open at a time; rachis to 2 mm long; peduncles 0–5 mm long, densely covered with appressed trichomes 0.16–0.25 mm long. *Flowers* with floral bracts 0.5–1 mm long, 0.4–0.6 mm wide at the base, ovate, with trichomes; pedicels 2–5 mm long, densely covered with flexuous trichomes 0.15–0.25 mm long. *Buds* 2.2–3 mm long, 1.5–1.7 mm diam., ovoid, with imbricate aestivation. *Calyx* fused for about ⅓ of its length; abaxial surface with trichomes; lobes 0.9–1.2 mm long, 0.6–0.8 mm wide, ovate, apically acute. *Corolla* cyathiform, basally fused; 2–3 mm long, abaxially and adaxially creamish green to yellow; lobes 1–1.3 mm wide, patent, oblong to lanceolate, apically obtuse to acute. *Corona* cyathiform, white, 1.8–2 mm high, equaling the gynostegium in height; C(is) consisting of Cs and Ci fused for ¾ to ⅞ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, broadly triangular, flat, apically reflexed. *Lobes of Ci* laminar, ovate to bifid, reflexed, with straight, entire margins. *Gynostegium* 2–2.5 mm high, 1.4–1.6 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, trapezoidal, abaxially planar; anther wings 0.7–0.8 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, centrifugal. Connective appendages 1–1.2 mm long, 0.8–1 mm wide, ovate, broader than the stamen, erect, inflated, with denticulate margins. *Pollinarium*: corpusculum 0.2–0.25 mm long, ovoid; caudicles 0.1–0.15 mm long, cylindrical, concavely recurved, thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, 0.45–0.55 mm long, 0.12–0.15 mm wide, oblongoid, ovate in cross section. *Stylar head* 0.8–1 mm diam., 1.2–1.3 mm high; upper part 0.9–1 mm high, capitate. *Follicles* one per flower, pendulous, 50–65 mm long, 4 mm diam., obclavate, apically strongly beaked, keeled, dark brown, with dense indument. *Seeds* 5.5–6 mm long, 3.5–4 mm wide, ovate, light to medium brown, seta and aseta side sculptured with longitudinal ridges, margins with 0.3–0.5-mm-wide wing with dentate margin; coma 20–23 mm long. *Chromosome number* unknown.

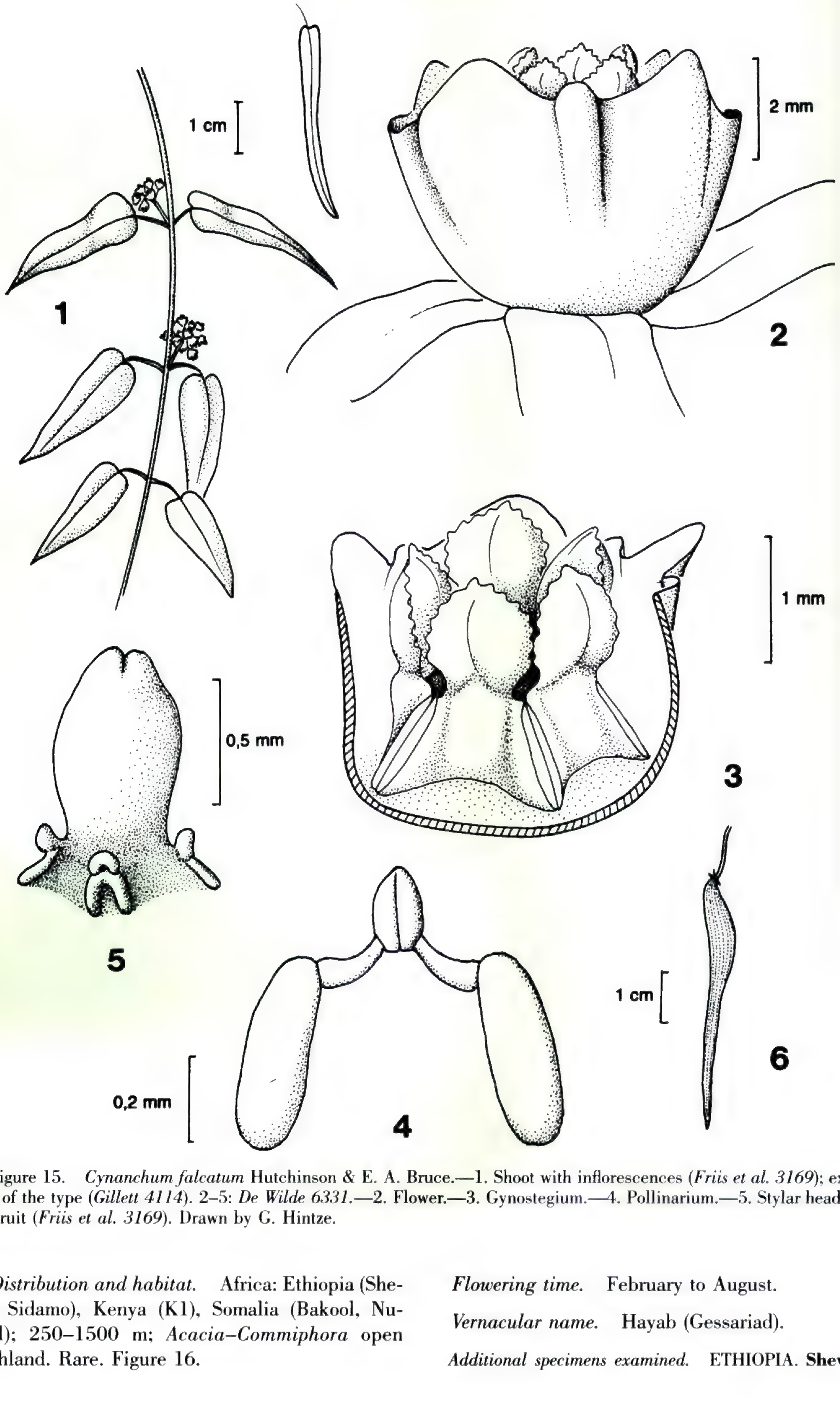


Figure 15. *Cynanchum falcatum* Hutchinson & E. A. Bruce.—1. Shoot with inflorescences (*Friis et al. 3169*); extra leaf of the type (*Gillett 4114*). 2–5: *De Wilde 6331*.—2. Flower.—3. Gynostegium.—4. Pollinarium.—5. Stylar head.—6. Fruit (*Friis et al. 3169*). Drawn by G. Hintze.

Distribution and habitat. Africa: Ethiopia (Shewa, Sidamo), Kenya (K1), Somalia (Bakool, Nugaal); 250–1500 m; *Acacia–Commiphora* open bushland. Rare. Figure 16.

Flowering time. February to August.

Vernacular name. Hayab (Gessariad).

Additional specimens examined. ETHIOPIA. **Shewa:**

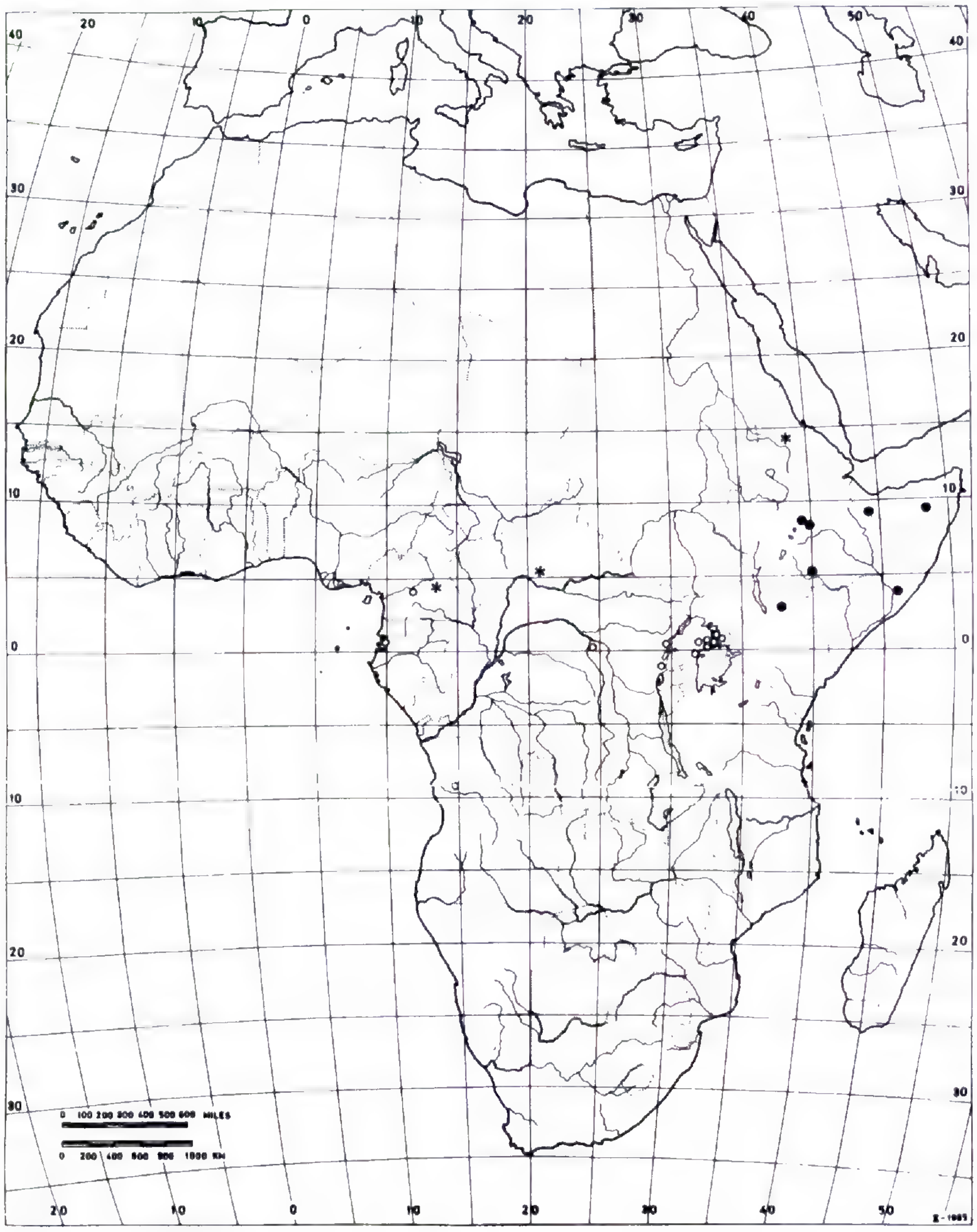


Figure 16. Known distribution of *Cynanchum falcatum* (dots), *C. heteromorphum* (asterisks), and *C. polyanthum* (open circles).

23 km N of Awash on rd. to Nazareth, ca. 1090 m, 30 Aug. 1967, *Westphal & Westphal-Stevels 1466* (K); 37 km NE Nazareth along rd. to Awash, ca. 1350 m, 4 Feb. 1970, *De Wilde 6331* (K, WAG). **Sidamo:** 40 km NE Neghelle along rd. to Filtu, 1450 m, 20 May 1982, *Friis, Mesfin & Vollesen 3169* (K). KENYA. **Northern Frontier:** Huri Hills, 25 Feb. 1963, *Bally 12526* (K). SOMALIA. Bakool, 22 km W of Mukwakori, 250 m, 13 June 1979, *Gillett, Hemming & Watson 22616* (K); Nugaal, Gardo–Hudun Rd., 950 m, 20 June 1981, *Gillett & Beckett 23533* (EA).

Comments. *Cynanchum falcatum* is close to *C. heteromorphum*, but the leaves are triangular and the corona more highly fused. The type is an unrepresentative specimen with very slender, falciform leaves, perhaps caused by disease. Most specimens exhibit leaves more like those widespread in the genus, while floral structure is the same.

11. Cynanchum galgalense Liede, sp. nov. TYPE: Somalia. Bari, Al Miskat Mts., ca. 15 km SW of Candala, Toh well, 800–850 m, 2 Dec. 1985, *Thulin 5612* (holotype, K; isotype, UPS). Figure 17.

Plantae foliis carnosulis marginibus incrassatis, inferioribus caducis; partibus staminalibus interstaminalibusque coronae gynostegialis late connatis, sulcatis, gynostegium obducenibus; capite stylorum tabulari.

Plants ascending, twining, 5–30 cm high, sparsely basicaulously branched. *Shoots* herbaceous, densely covered with erect trichomes 0.1–0.12 mm long, basally slightly woody, with yellowish to brownish bark; internodes 10–50 cm long, 0.7–1.2 mm diam. "*Stipules*" absent. *Leaves* caducous, the upper ones sessile, lower ones with

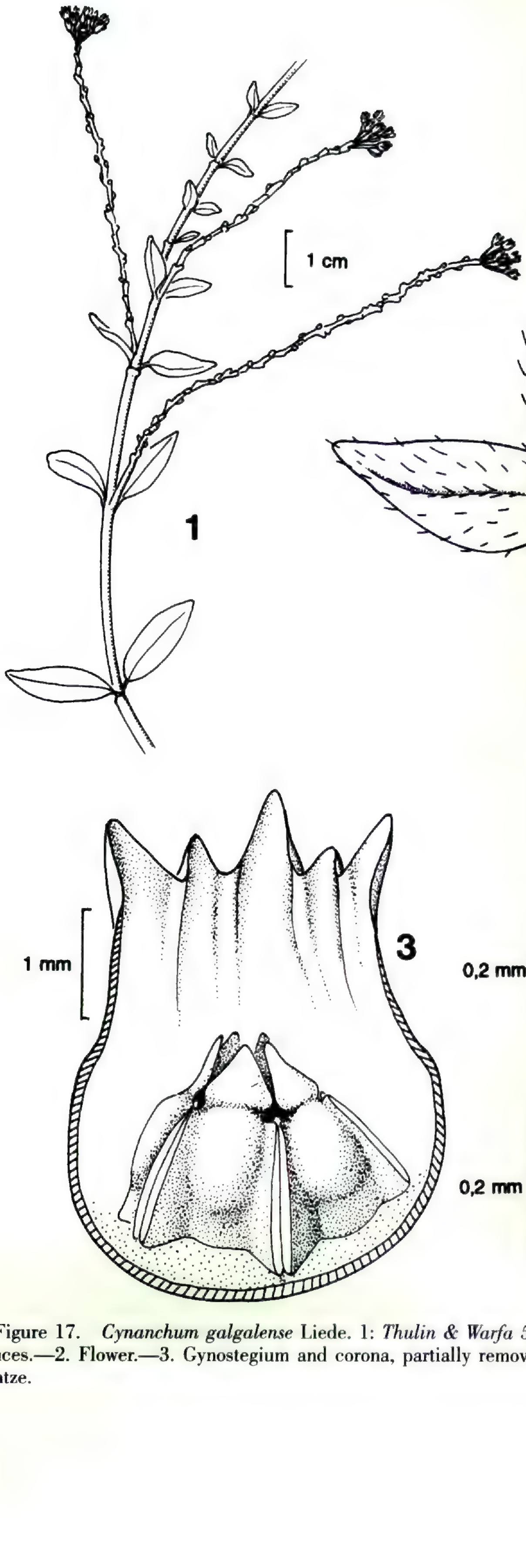


Figure 17. *Cynanchum galgalense* Liede. 1: *Thulin & Warfa 5612*; 2–5: *Newbould 1095*.—1. Habit with inflorescences.—2. Flower.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head. Drawn by G. Hintze.

petioles to 5 mm long; leaf blades fleshy, 4–14 mm long, 2–9(–13) mm wide, elliptic, basally rounded, without colleters, apically acute, margins straight and thickened, adaxially and abaxially sparsely to densely covered with erect trichomes 0.1–0.12 mm long, evenly distributed over the whole surface. *Inflorescences* bostrychoid, 5–24-flowered, all flowers open at a time; rachis 5–50 mm long; peduncles 5–7 mm long, densely covered with erect trichomes 0.1–0.15 mm long. *Flowers* with floral bracts 1–1.2 mm long, 0.1–0.2 mm wide at the base, linear, with trichomes; pedicels 3–4 mm long, sparsely covered with erect trichomes 0.1–0.12 mm long. *Buds* 1.4–1.5 mm long, 1 mm diam., conical, with imbricate aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 0.8–1 mm long, 0.4–0.5 mm wide, ovate, apically acute. *Corolla* cyathiform, basally fused; 1.5–1.7 mm long, abaxially and adaxially cream-colored; adaxially with verrucose trichomes 0.04–0.05 mm long, evenly distributed over the whole surface; lobes 0.5–0.7 mm wide, incurved to patent, ovate to oblong, apically acute. *Corona* urceolate, ivory, ca. 0.8 mm high, exceeding the gynostegium and partly obscuring it; C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, Cs and Ci differentiated, Ci as long as Cs. *Cs* basally just adnate to the filaments, without adaxial appendages; lobes of Cs laminar, ovate, producing a pronounced convex fold along the upper half of corona length, apically erect. *Lobes of Ci* laminar, oblong, producing a pronounced convex fold along the upper half of corona length, erect to reflexed, with straight margins. *Gynostegium* sessile, 0.9–1 mm high, 1–1.1 mm diam. Anthers broader than high, trapezoidal, abaxially convex; anther wings 0.7–0.8 mm long, convergent, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.3–0.4 mm long, 0.3–0.4 mm wide, ovate, narrower than the stamen, strongly inflexed. *Pollinarium*: corpusculum ca. 0.15 mm long, elliptic, margins of the corpuscular cleft basally widened; caudicles ca. 0.05 mm long, flattened, concavely recurved, trapezoid; pollinia subapically attached to the caudicles, 0.11–0.12 mm long, 0.045–0.055 mm wide, elliptical in cross section, oblongoid. *Stylar head* 0.35–0.4 mm diam., 0.2–0.25 mm high; upper part 0.08–0.1 mm high, equaling the lower part in height, tabular. *Follicles* one per flower, ca. 30 mm long, 4 mm diam., fusiform, apically acute but not beaked, light brown, smooth, isolatedly covered with trichomes, with papery pericarp. *Seeds* and *chromosome number* unknown.

Distribution and habitat. Africa: Somalia (Bari, Nugaal, Sanaag); 800–2600 m; in rock crevices of limestone cliffs. Localized and rare. Figure 2.

Flowering time. July, November to December.

Vernacular name. Darjo.

Additional specimens examined. SOMALIA. Bari, Galgalo, 1000–1150 m, 1 Dec. 1986, *Thulin & Warfa 6205* (K, UPS); above Galgalo, ca. 1150 m, 27 Nov. 1971, *Lavranos 9014* (K); Nugaal, Elalo, Tukalamis, *Newbould 1095* (K); Sanaag, Surud Range, N of Erigavo, 1900–2060 m, 8 July 1981, *Gillett & Watson 23843* (K).

Comments. *Cynanchum galgalense* is a very unusual species, but most likely a *Cynanchum* with verrucose, sparse trichomes on the adaxial side of the corolla lobes and a highly fused corona. Probably related to *C. obtusifolium* and its allies. White latex would confirm its position in the genus.

12. Cynanchum gerrardii (Harvey) Liede, Taxon 40: 117. 1991. *Sarcocyphula gerrardii* Harv., Thes. Cap. 2: 58, t. 191. 1863. TYPE: South Africa. Natal: Tugela, *Gerrard 1321* (holotype, TCD; isotype, BM).

Cynanchum sarcostemmatoides K. Schum. in Engl., Pflanzenw. Ost-Afrikas C, 323. Aug. 1895. *Cynanchum sarcostemmoides* K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 252. Oct. 1895. (orth. var.). TYPE: Tanzania. Tanga: Amboni, June 1893, *Holst 2706* (lectotype, designated by Liede (1993), K).

Plants ascending, twining, 0.5–2 m high, richly acrocaulously branched; subterranean organs consisting only of fibrous roots. *Shoots* perennial, semisucculent, finely striate, obscurely glaucous, glabrescent, isolatedly covered with appressed multicellular trichomes 0.2–0.4 mm long, basally corky, with thin, yellowish bark; internodes (2–)4–8(–10) cm long, 1.5–2.5 mm diam. Latex white to slightly ivory. *Leaf scales* often not exactly opposite, 0.8–1.2 mm long, 0.5–0.8 mm wide, apically acute. *Inflorescences* bostrychoid to sciadioidal, 4–7-flowered, 2–4 flowers open at a time; rachis to 4 mm long; peduncles 0–2.5 mm long, sparsely covered with appressed trichomes 0.2–0.4 mm long. *Flowers* sweetly scented, nectariferous; floral bracts 0.2–0.5 mm long, 0.5–0.6 mm wide at the base, deltoid, with trichomes; pedicels 3–4.5 mm long, glabrous. *Buds* 0.4–0.5 mm long, 0.3–0.4 mm diam., globose to ovoid, with imbricate aestivation. *Calyx* basally fused; abaxial surface glabrous; lobes 0.3–0.4 mm long, 0.5–0.6 mm wide, ovate to triangular, apically acute. *Corolla* rotate, petals fused for about a quarter of their length; 2–3 mm long, abaxially green to white, adaxially green; lobes 1–1.5 mm wide, declinate, ovate, apically acuminate. *Corona* white,

cyathiform, 1.2–1.5 mm high, slightly exceeding the gynostegium. *C(is)* consisting of Cs and Ci fused for ¾ to ⅞ of total corona height, only Cs differentiated, Ci thinner than Cs. *Cs* adnate to the filaments, appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, triangular, apically erect to inflexed, with straight margins. *Gynostegium* sessile, 1.2–1.5 mm high, 0.8–1.2 mm diam. *Stamens* with free filaments 0.6–0.8 mm long. Anthers broader than high, trapezoidal, abaxially planar to convex; anther wings 0.3–0.4 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings divergent toward the base, in the same plane as the anther. Connective appendages 0.38–0.42 mm long, 0.5–0.55 mm wide, ovate to triangular, narrower than the stamen, strongly inflexed. *Pollinarium*: corpusculum ca. 0.15 mm long; caudicles 0.1–0.12 mm long, flattened, straight, declinate, triangular, thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, 0.4–0.45 mm long, 0.15–0.2 mm wide, ovoid, round in cross section. *Stylar head* white, 0.8–0.85 mm diam., 0.25–0.3 mm high; upper part 0.2–0.23 mm high, flat to depressed-conical. *Follicles* one, occasionally two per flower, 85–120 mm long, 6–8 mm diam., elongated, round in cross section, apically short beaked, light brown to dark brown, smooth, glabrous. *Seeds* 5–6 mm long, 2–3 mm wide, pyriform, medium brown; seta and aseta side with regularly arranged papillae and trichomes 0.3 mm long, wingless, margins entire; coma 20–25 mm long. *Chromosome number*: $2n = 22$ (voucher: *Noltee 995*, MSUN).

Distribution and habitat. Arabian Peninsula: Saudi Arabia, Yemen. Africa: Eritrea, Ethiopia (Gamo Gofa, Shewa, Sidamo); Kenya (K1, K2, K4, K5, K6, K7), Somalia (Sanaag, Woqooyi Galbeed), South Africa (Cape, Natal, Transvaal), Tanzania (T2, T3, T6, T7), Uganda (U1, U4), Zaïre, Zambia, Zimbabwe. Mascarene Islands: Comores, Madagascar (Antsiranana, Toliara). 0–1500 m; close to the sea or further inland, on rocky outcrops, in sandy or clayey depressions, often in slightly disturbed sites. Very widespread, but not frequent. Figure 18.

Flowering time. All year; mostly after rains.

Vernacular names. Debina Dir (Somalia); Kipagoro (Kitamba), Melktou (South Africa).

Uses. Zulus eat young shoots; in East Africa used as fish poison; in Somalia eaten, much liked by pregnant women (*Gillett 3939*).

Selected specimens examined. ETHIOPIA. **Gamo Gofa:** 27.5 km S of Arba Minch, 1150–1300 m, 3 Aug. 1975, *Gilbert, Thulin & Aweke 330* (K, MO, UPS). **Shewa:** ca. 40 km E of Nazareth, ca. 1200 m, 5 Apr. 1966, *De Wilde & De Wilde-Duyfjes 10519* (K, MO). **Sidamo:** 1 km N of Harekelo along rd. to Kebre Mengist 1450 m, 24 May 1982, *Friis, Tadesse & Vollesen 3292* (K). KENYA. **Central:** Kitui, 1 mi. N of Kangonde on Kangonde–Embu rd., 8 May 1960, *Napper 1664* (K); Machakos, Kibwezi Plains, 1000 m, 15 May 1938, *Bally 8333* (K). **Coast:** Kilifi, Malindi Golf Course, 10 m, 22 Sep. 1989, *Robertson 5914* (K); Kwale, Kilibasi Hill, 450–827 m, 19 Nov. 1989, *Luke & Robertson 2105* (K); Mombasa, Port Tudor, Mombasa, 660 m, Oct. 1931, *MacNaughtan 26* (K); Tana River, Kurawa, 30 mi. S of Garsen, 15 m, 25 Sep. 1961, *Polhill & Paulo* 569 (K); Taita, Voi, 660 m, 11 May 1931, *Napier 1064* (K); Masai, SW of Ngong hills, 1860 m, 4 Aug. 1968, *Gillet 18689* (K). **Nyanza:** South Kavirondo, Homa Mountain, 2 Dec. 1934, *Turner 6628* (K, MO); Turkana, 1 km NE of Loiya on Lodwar rd., 1075 m, 8 Nov. 1977, *Carter & Stannar 264* (K). MOZAMBIQUE. Cabo Delgado, Pemba, 12 Aug. 1983, *Groenendijk & Dunge 566* (MO); Manica & Aofala, between Divinhe & Cherinda, 2 Sep. 1961, *Leach 11258* (K, MO, SRHG); Maputo, Marracuene, Macaneta, 5–10 m, 1 Aug. 1980, *Schäfer 7218* (K, MO); Zambezia, 20 mi. N of Quelimane, 20 Aug. 1962, *Wild 5877* (K, MO, SRHG). SOMALIA. Sanaagh, Surud, 1973, *Bally & Melville s.n.* (K); Woqooyi Galbeed, Hargesia, 1130 m, 21 Sep. 1932, *Gillett 3939* (K). SOUTH AFRICA. **Cape:** Albany, N of Pluto's Vale, 11 Apr. 1954, *Noel 1544* (GRA); Alexandria, Zuurkop, Addo National Park, 330 m, 18 Oct. 1951, *Archibald 3854* (GRA); Butterworth, along the Kei River, Jan. 1892, *Flanagan 1038* (BOL, SAM); Grahamstown, Piggott Bridge, 265 m, 13 Apr. 1978, *Bayliss 8474* (MO); Jansenville, Gannahoek, 8 May 1985, *Hoffman 791* (GRA); Peddie, banks of Fish River, 600 m, 15 Mar. 1970, *Bayliss 4554* (MO); Port Elizabeth, Farm Vaalkrans, 600 m, 1 June 1972, *Bayliss 5100* (MO); Somerset East, Zuurberg, 20 Nov. 1947, *Barker 4928* (NBG); Steytlerville, 2 km S of Mt. Stewart toward Steytlerville, 8 Dec. 1978, *Bruyns 1887* (NBG); Stutterheim, prope Kingwilliamstown, Dec. 1870, *Munsel-Weale s.n.* (SAM 18599, SAM). **Natal:** Durban, Durban, Bluff, 23 Apr. 1914, *Wood 12613* (PRE); Lower Tugela, Lower Tugela valley opposite Gnembe River confluence, ca. 170 m, 27 Feb. 1963, *Edwards 3048* (PRE); Nkandhla, Nogeya, Umhlatuzi Valley, 31 May 1967, *Venter 3708* (PRE); Port Shepstone, Oriba Flats, Umzimkulu Gorge, Apr. 1937, *McClean 408* (MO, PRE); Ubombo, Jozini, 16 Apr. 1968, *Strey 8128* (PRE). **Transvaal:** Selati River, Eastern Transvaal, *Rogers 2661a* (BOL). SWAZILAND. Louwsburg, Maloma, ca. 500 m, 5 Sep. 1963, *Dlamini s.n.* (NBG 71759, NBG); Mbabane, near Croydon, 9 Sep. 1957, *Compton 27031* (NBG); Stegi, Mhlumeni Border Station, 22 mi. NE of Stegi, 330 m, 4 June 1947, *Codd & Dyer 2929* (PRE). TANZANIA. **Arusha:** Kemosomu gorge, 1660 m, 19 Feb. 1971, *Richards & Arasululu 26688* (K). **Iringa:** top of Kitonga gorge, Image mountain, 1200–1800 m, 9 Dec. 1986, *Lovett & Congden 1070* (K, MO). **Morogoro:** Uluguru Gebirge, 500 m, 6 June 1933, *Schlieben 3993* (B); Moshi, Kikafu River bridge, 15 Apr. 1968, *Bigger 1773* (EA). **Pwani:** Mafia Island, Tretole, 2 Aug. 1932, *Schlieben 2620* (B). **Tanga:** Sawa, sea level, 3 Sep. 1956, *Faulkner 1914* (K). **Zanzibar:** M'beoni, sea level, 26 June 1960, *Faulkner 2624* (K). UGANDA. Bunyoro, Budongo Forest, July 1936, *Eggeling 3069* (K); Karamoja, near Amudat, 1330 m, *Wilson 858* (K). ZAÏRE. Ruindi, Oct. 1937, *Lebrun 8000* (K); Katanda, Sep. 1937,

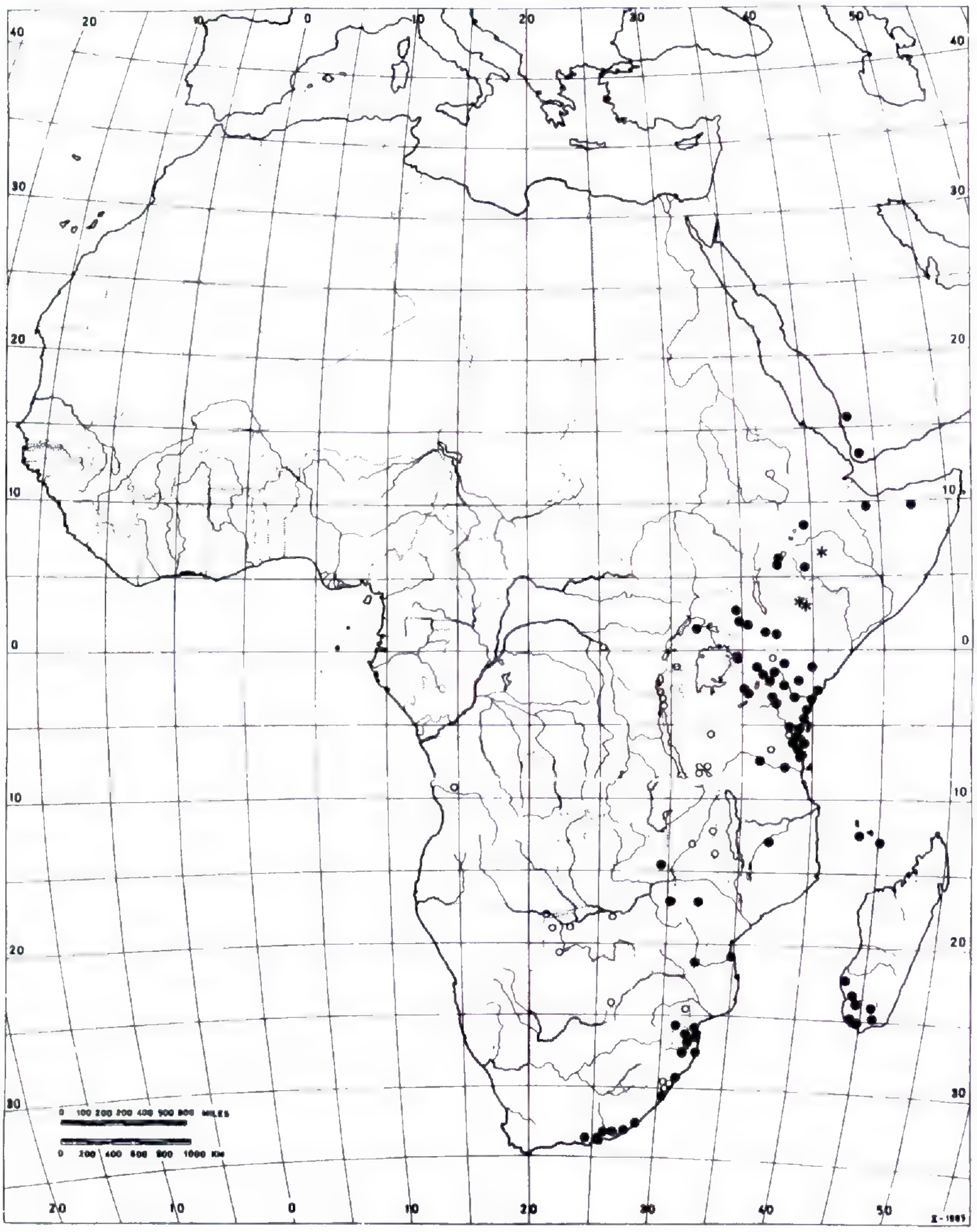


Figure 18. Known distribution of *Cynanchum gerrardii* (dots), *C. lenewtonii* (asterisks), and *C. schistoglossum* (open circles).

Lebrun 7702 (K); May-yo-moto, Sep. 1937, *Lebrun 9217* (K); Mwuvito et la Kamakaba, Jan. 1938, *Lebrun 9694* (K). ZAMBIA. Lusaka, 8 Mar. 1971, *Fanshawe 11191* (K). ZIMBABWE. Chiredzi, Chuanja Hill, Lona-re Zhau Game Reserve, 27 May 1971, *Ngoni 134* (MO); Mandula, Whindale Ranch, Mandula, above farm-house, ca. 1000 m, 24 Mar. 1969, *Leach, Biegel & Pope 14328* (K, MO, SRGH); Mtoko, Kopje near village, 4 Dec. 1960, *Wild 5287* (K, MO); Wankie, Inyantue sale pens, ca. 915 m, 24 Mar. 1969, *Leach 11630* (K, SRGH); Nuanetsi, near Kapatenis, 65 km NE of Malvernia, 25 Apr. 1962, *Drummond 7718* (K, SRGH).

Comments. Throughout its history, several names have been applied to *Cynanchum gerrardii.* Of these, *Cynanchum aphyllum* (Thunb.) Schltr. is not an available name for this species, because *Asclepias aphylla* Thunb. [Prod. Fl. Cap. 47 (1794)], a later homonym of *A. aphylla* Forssk., has been lectotypified (Liede, 1991) in such a way that it is a synonym of *Sarcostemma viminale* (L.) R. Br.

Likewise, *Cynanchum tetrapterum* (Turcz.) R. A. Dyer ex Bullock [Kew Bull. 10: 624. 1955] is based on *Sarcostemma tetrapterum* Turcz., which has been lectotypified (Liede, 1991) on a specimen representing *Sarcostemma viminale* (L.) R. Br. sensu lato.

Vincetoxicum sarcostemmoides Schweinf. ex Penzig [Atti Congr. Bot. Int. Genova 349 (1893), nomen nudum] also represents this *C. gerrardii* (fide Bullock, 1955).

An extremely adaptable species, also easy to cultivate. The affinities of *C. gerrardii* clearly lie with a group of leafless Malagasy species.

Further details, illustration, and a detailed southern African distribution map are provided in Liede (1993).

13. Cynanchum gonoloboides Schlechter, Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot. 2: 543. 1913. TYPE: Rwanda: *Schlechter 1617* (holotype, B presumably destroyed). NEOTYPE: Kenya. Rift Valley: Nakuru, Doboti, about 9 mi. from Cobb's gate near the Mau Forest Reserve on the track to Nairagie Ngare, 3200 m, *Glover, Gwynne & Samuel 1492* (neotype, designated here, K; isoneotypes, EA, FT). Figure 19.

Plants ascending, twining, 4–5 m high, richly and irregularly branched, rhizomatous; subterranean organs woody rootstocks, 7–9 cm diam. *Shoots* perennial, herbaceous, glabrescent, densely covered with flexuous trichomes 0.4–0.5 mm long, when young; basally woody, with yellowish bark, internodes 7–20 cm long, 2.5–3 mm diam. "*Stipules*" absent. *Leaves* with petioles 12–20(–40) mm long, leaf blades herbaceous, 55–90 mm long, 35–60 mm wide, ovate, basally cordate with 8–12 colleters in the adaxial sinus, apically acuminate, apiculus 4–10 mm long, adaxially densely covered with flexuous trichomes 0.2–0.25 mm long, evenly distributed over the whole surface (when young), abaxially densely covered with flexuous trichomes 0.4–0.5 mm long, restricted to veins and margins (when young). *Inflorescences* bostrychoid, 6–15-flowered, 3–7 flowers open at a time; rachis 5–30 mm long; peduncles 15–25(–30) mm long, sparsely covered with flexuous trichomes 0.25–0.35 mm long. *Flowers* pleasantly honey-scented; floral bracts 2–2.5 mm long, 0.5–0.7 mm wide at the base, linear to triangular, with trichomes; pedicels 10–22 mm long, densely covered with flexuous trichomes 0.15–0.25 mm long. *Buds* 3.5–4 mm long, 4–4.5 mm diam., globose, with imbricate aestivation. *Calyx* basally fused; abaxial surface densely covered with trichomes; lobes 3.5–4 mm long, 2–2.5 mm wide, ovate, apically acuminate. *Corolla* rotate, basally fused, 4–5 mm long, abaxially and adaxially greenish yellow, brown along the main nerves, often also basally; lobes 2–2.5 mm wide, horizontal to declinate, oblong, apically acute. *Corona* white, 3.5–4 mm high, equaling the gynostegium in height, C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, only Cs differentiated. *Cs* not adnate to the filaments, adaxially with a basal protuberance corresponding to the lower margin of the anther proper, without adaxial appendages; lobes of Cs laminar, trifid (the medium lobe widely ovate, occupying about ⅔ of the total width, the lateral lobes triangular), apically inflexed. *Gynostegium* 1.2–1.3 mm high, 3.5–3.7 mm diam., atop a stipe, 1.5–1.7 mm long. *Stamens* without free filaments, anthers broader than high, deltoid, abaxially convex; anther wings 0.35–0.4 mm long, parallel to each other, not extending along the whole length of the anther; the anther forming a "pseudostipe," of 0.2–0.25 mm height, adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.75–0.8 mm long, 1.4–1.5 mm wide, ovate, narrower than the stamen, strongly inflexed, with emarginate margins. *Pollinarium*: corpusculum 0.35–0.4 mm long; caudicles 0.8–0.9 mm long, cylindrical, s-shaped, concave-convex, horizontal; pollinia laterally attached to the caudicles, 0.35–0.4 mm long, 0.24–0.26 mm wide, globose to ovoid, ovate in cross section. *Stylar head* white to cream, 2.25–2.5 mm diam., 0.35–0.4 mm high; upper part flat. *Follicles* ca. 110 mm long, 15 mm diam., obclavate, round in cross section, apically acute, wingless, light brown, isolatedly covered with short protuberances, with thick pericarp. *Seeds* 9–11 mm long, 4–6 mm wide, ovate, medium brown, seta side smooth, marginally with 0.4 mm wide wing, coma 20–25 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Ethiopia (Sidamo), Kenya (K3, K4); Rwanda, Tanzania (T6); 2800–3800 m; bamboo forest. Rather localized, but neither rare nor endangered. Figure 10.

Flowering time. January to April.

Vernacular name. Ol'obito (Masai).

Additional specimens seen. ETHIOPIA. **Sidamo:** Mt. Delo, Amaro Mts., 3400 m, 28 Jan. 1953, *Gillett 14973* (EA). KENYA. **Central:** Nyeri, Aberdares Nat. Park Rd., Nyeri end, 2900 m, *Agnew 7179* (EA). **Rift Valley:** Elgeyo, Charanqui Hills, Embobut forest, in Arorr & Embobut valleys, 3460–3800 m, Jan. 1971, *Tweedie 3912* (K); Trans Nzoia, N. E. Elgon, top of Arawa Forest, ca. 2860 m, Feb. 1961, *Tweedie 2103* (BR, K).

Comments. The type specimen [Rwanda. Karissimbi, ca. 2500 m, Nov. 1907, *Schlechter 1617*] could not be found and was most probably destroyed in B. The description of the species, however, clearly matches Sp. A in Agnew (1974: 387) with *C. gonoloboides.* Therefore, Schlechter's old name is neotypified here. Despite its highly fused corona and the distinctive stipe, the species is easily identified as a sister species of *C. balense.*

14. Cynanchum heteromorphum Vatke, Linnaea 40: 215. 1876. TYPE: Ethiopia. Tigray: Hamedo plain, 1530 m, 31 Aug. 1862, *Schimper 940* (holotype, B presumably destroyed; lectotype, designated here, K). Figure 20.

Cynanchum fraternum N. E. Br., Bull. Misc. Inform., Kew

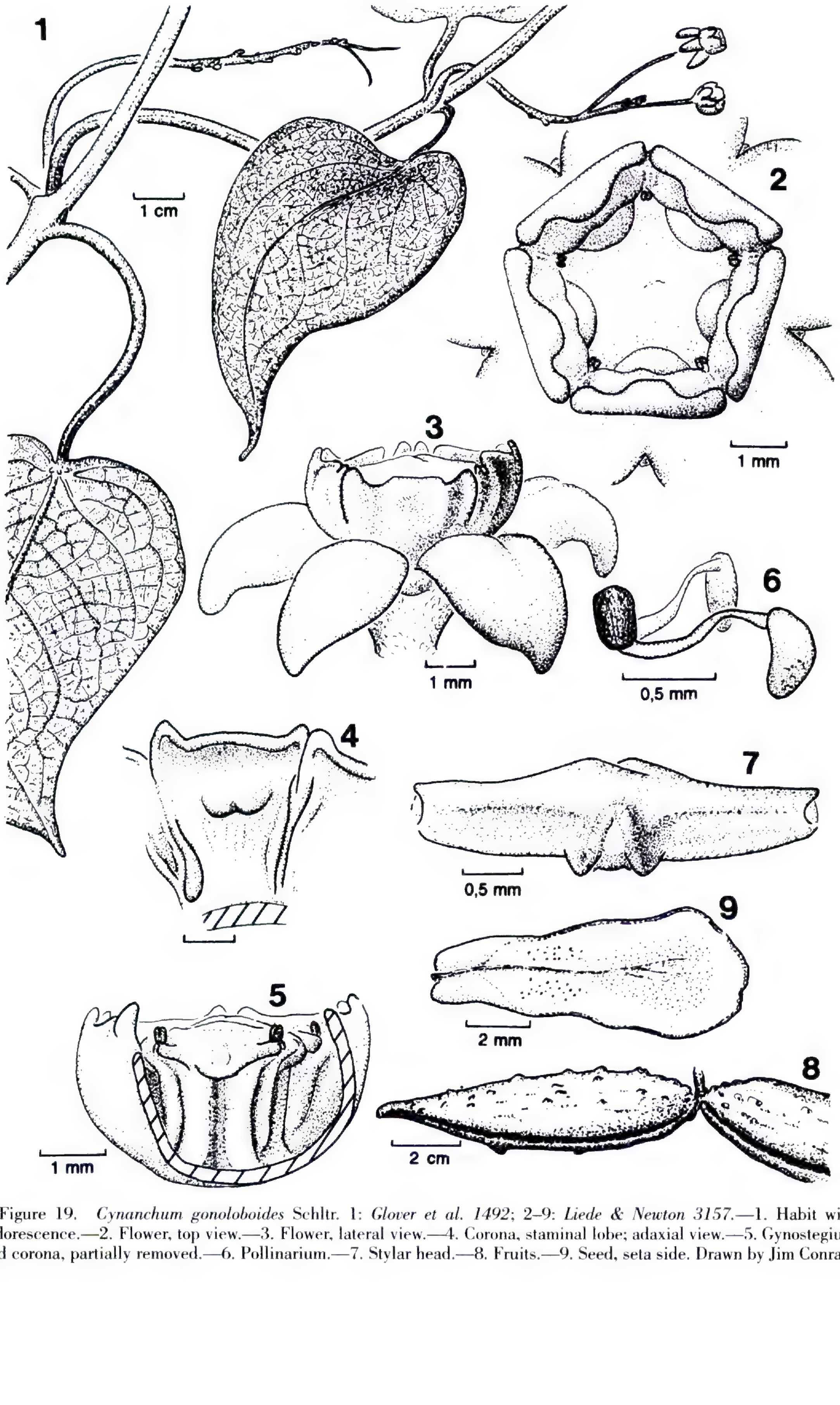
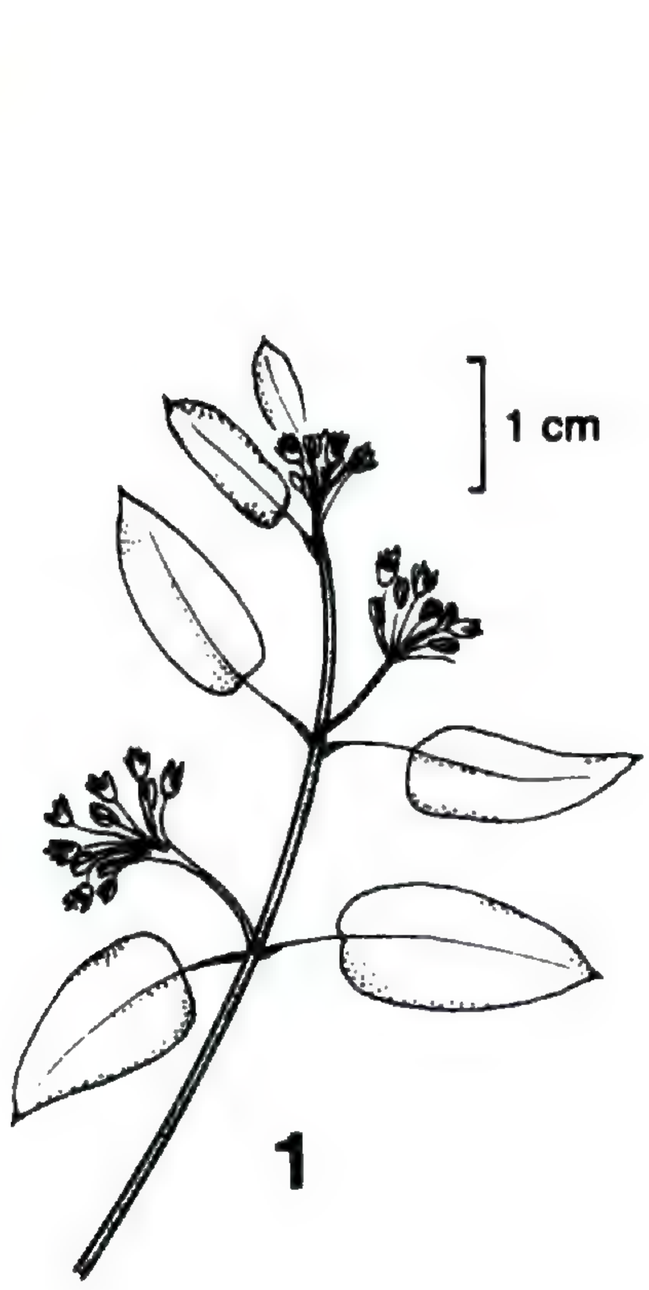


Figure 19. *Cynanchum gonoloboides* Schltr. 1: *Glover et al. 1492*; 2–9: *Liede & Newton 3157*.—1. Habit with inflorescence.—2. Flower, top view.—3. Flower, lateral view.—4. Corona, staminal lobe; adaxial view.—5. Gynostegium and corona, partially removed.—6. Pollinarium.—7. Stylar head.—8. Fruits.—9. Seed, seta side. Drawn by Jim Conrad.



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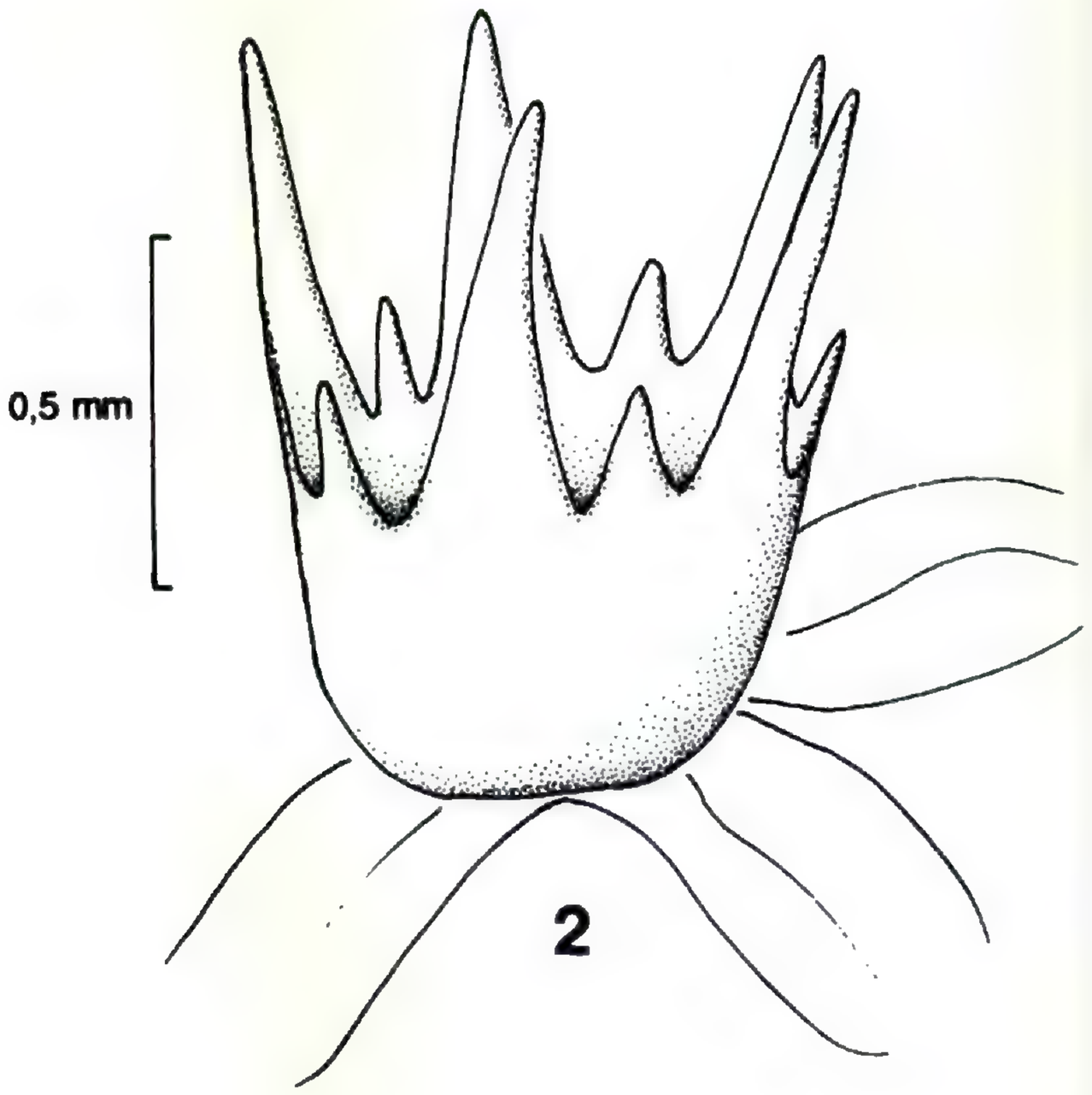

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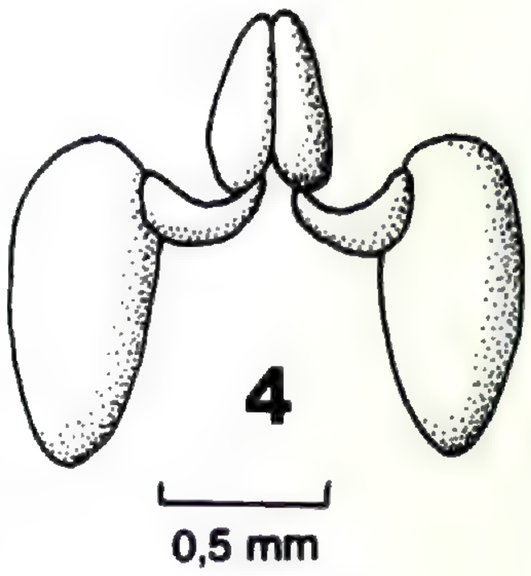

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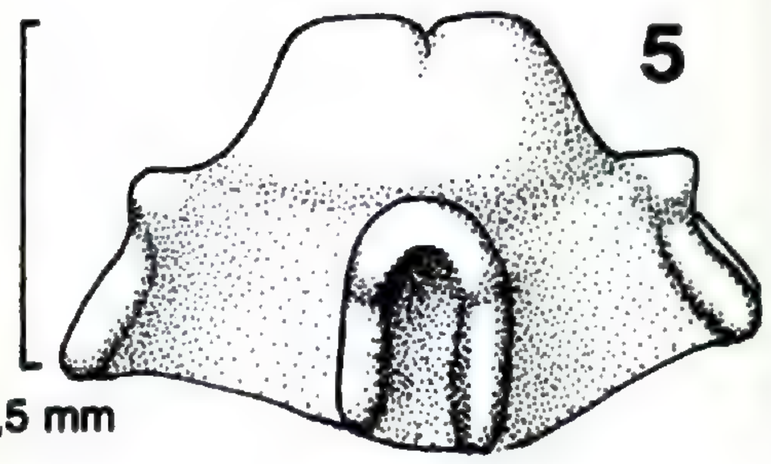

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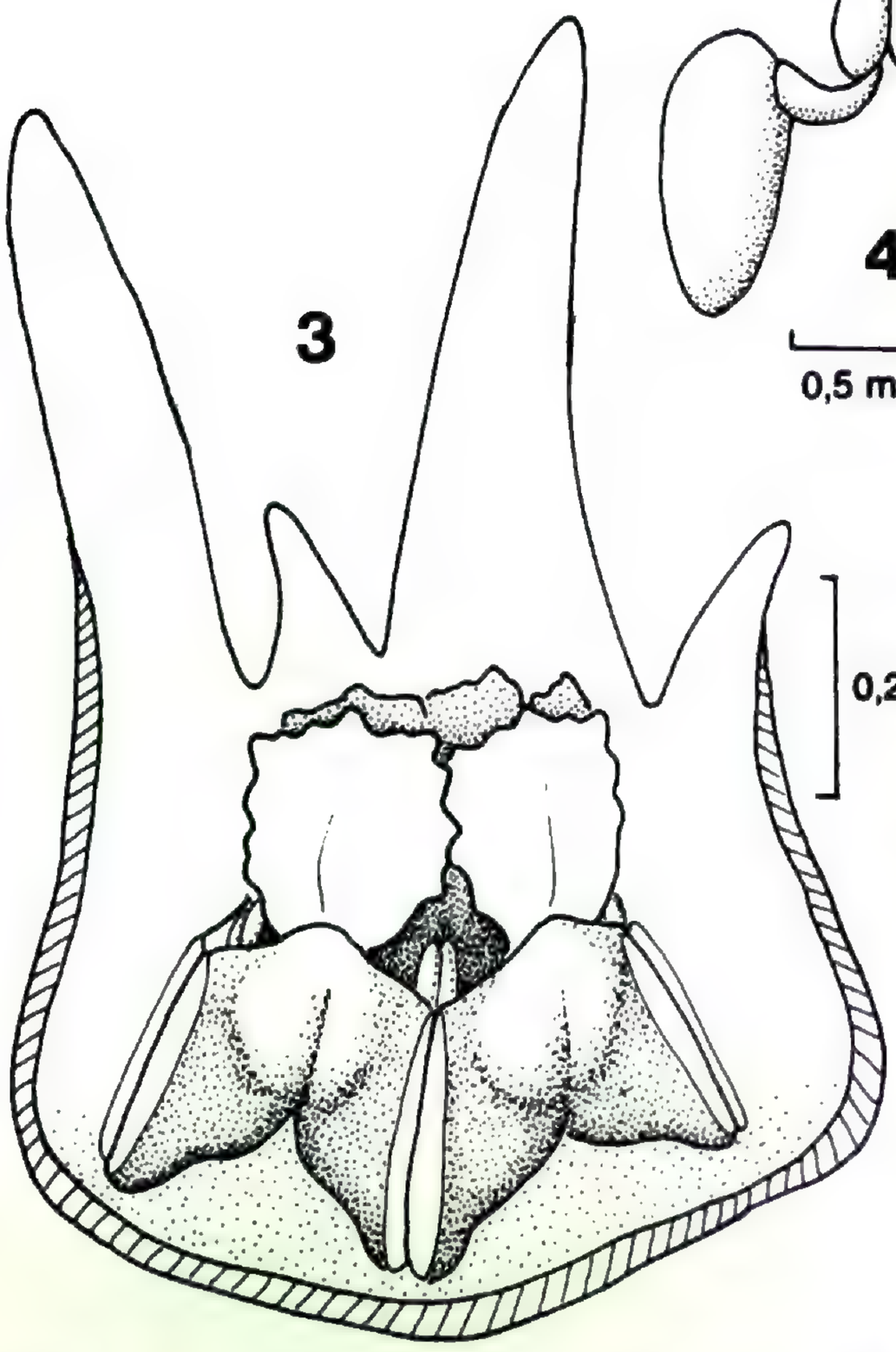

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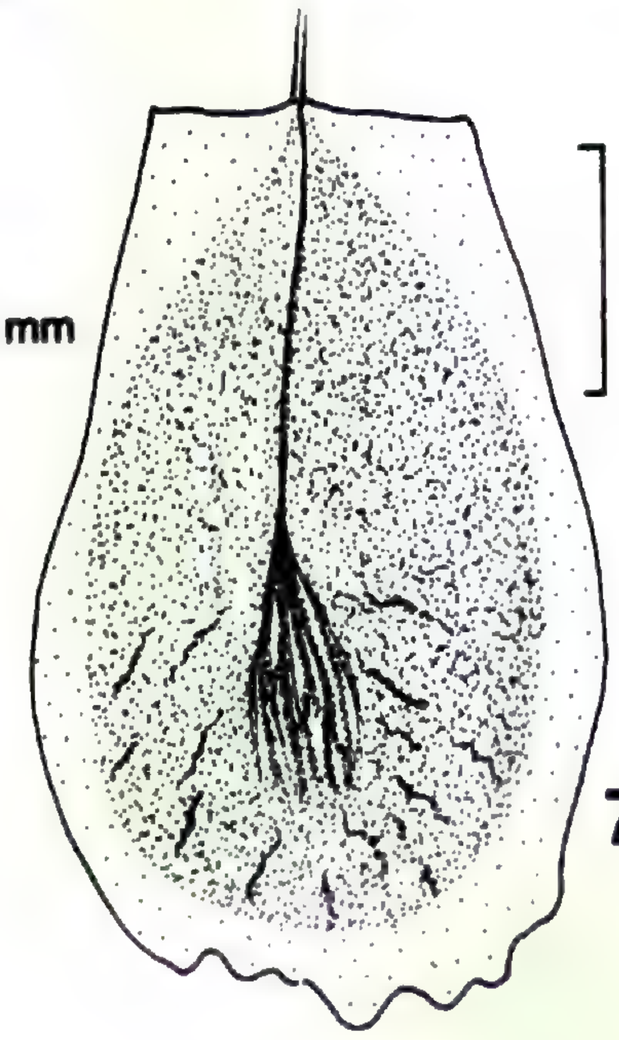

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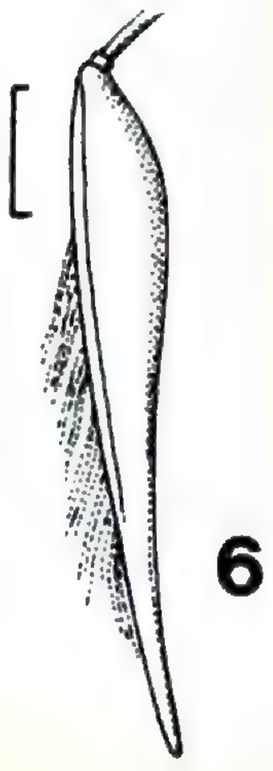

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Figure 20. *Cynanchum heteromorphum* Vatke. 1–5: *Schimper 1802;* 6, 7: *Schimper 940.*—1. Shoot with inflorescences.—2. Flower.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head.—6. Fruit.—7. Seed, seta side. Drawn by G. Hintze.

106: 256. 1895. TYPE: Ethiopia. Tigray: Djeladjeranne, 24 Oct. 1840, *Schimper s.n.* (holotype, B presumably destroyed; lectotype, designated here, K).

Cynanchum pleianthum K. Schum., Annuario Reale Ist. Bot. Roma 7: 39. 1898. TYPE: Somalia. Locis paludosis in Pianure di Savati, 25 Nov. 1893, *Ruspoli & Riva 1533* (holotype, B presumably destroyed; lectotype, designated here, FT).

Plants ascending, twining, sparsely branched. *Shoots* herbaceous, sparsely glabrescent with appressed trichomes 0.25–0.3 mm long; internodes 6.5–10 cm long, 0.8–1.1 mm diam. "*Stipules*" absent. *Leaves* with petioles 6–8 mm long; leaf blades herbaceous, 18–32 mm long, 8–14 mm wide, ovate, basally rounded to obtuse with 5 colleters adaxially, apically acute to acuminate, apiculus 0.5–1 mm long, adaxially isolatedly covered with appressed trichomes 0.25–0.3 mm long, evenly distributed over the whole surface, abaxially with appressed trichomes 0.25–0.3 mm long, concentrated on veins and margins. *Inflorescences* bostrychoid, 8–10-flowered, 3–5 flowers open at a time; rachis 1–3 mm long; peduncles 7–9 mm long, densely covered with appressed trichomes 0.15–0.18 mm long. *Flowers* with floral bracts 0.6–0.7 mm long, 0.3–0.5 mm wide at the base, triangular; pedicels 4–6 mm long, sparsely covered with appressed trichomes 0.15–0.2 mm long. *Buds* 1.8–2 mm long, 1.3–1.5 mm diam., ovoid, with imbricate aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 1–1.2 mm long, 0.5–0.6 mm wide, ovate, apically acute. *Corolla* cyathiform, basally fused; 2.5–3 mm long; lobes 0.8–1 mm wide, patent, oblong, apically obtuse. *Corona* cyathiform, 3 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci fused for a little less than ½ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, elongate-triangular, apically reflexed. *Lobes of Ci* laminar, oblong, flat, reflexed. *Gynostegium* 1.8–1.9 mm high, 1.8–1.9 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, rectangular, abaxially planar; anther wings 0.9–1 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.65–0.7 mm long, 0.7–0.75 mm wide, ovate, narrower than the stamen, erect, with dentate margins. *Pollinarium*: corpusculum 0.2 mm long, about as long as broad, rhomboid; caudicles 0.12–0.15 mm long, cylindrical, concavely recurved; pollinia subapically attached to the caudicles, 0.35–0.4 mm long, 0.15–0.17 mm wide, oblongoid, ovate in cross section. *Stylar head* 0.7–1 mm diam., 0.5–0.6 mm high; upper part 0.25–0.3 mm high, umbonate. *Follicles* one per flower, pendulous, 50–65 mm long, 7–8 mm diam., obclavate, obtusely deltate in cross section, apically strongly beaked, keeled, light brown, longitudinally grooved, sparsely covered with trichomes. *Seeds* 4–5 mm long, 2.5–3 mm wide, ovate, medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.4–0.5 mm wide wing with dentate margin; coma 15–20 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Cameroon, Central African Republic, Eritrea, Ethiopia (Tigray), Somalia; around 1600 m, on sandy soil. Very rarely collected and even less so in recent years; presumably endangered. Figure 16.

Flowering time. October to November.

Additional specimens examined. CAMEROON. Bertoua, near Catholic mission, 5 Nov. 1960, *Breteler 615* (K, WAG). CENTRAL AFRICAN REPUBLIC. Krébidjé (Fort Sibut), vallée de la moyenne Tomi, 6 Oct. 1902, *Chevalier 5649* (P). ERITREA. Medri od Tesfa. Adi Ghebsus, 1600 m, 2 Nov. 1906, *Pappi 7300* (FT).

Comments. The flower of *Cynanchum heteromorphum* is quite similar to that of *C. falcatum*; however, the clavate stylar head and the pronouncedly triangular leaves of the latter are unmistakable. With *C. clavidens* subsp. *hastifolium*, this taxon shares the unusual East African–West African disjunction.

15. Cynanchum ledermannii Schlechter Bot. Jahrb. Syst. 51: 140. 1913. TYPE: Burundi. Bubanza, Mugomero (Rugazi), 2000 m, 2 May 1981, *Reekmans 10069* (neotype, designated here, K). Syntypes cited in the protologue: Cameroon. Northern: Banso Mtns., ca. 2000 m, Oct. 1909, *Ledermann 5757*; Muti-slopes, near Mfongu, 1700–1800 m, Oct.–Nov. 1909, *Ledermann 5892, 5931a* (all probably destroyed in B, no isotypes found). Figure 21.

Plants ascending, twining, to 3 m high, richly and irregularly branched. *Shoots* perennial, herbaceous, sparsely covered with flexuous trichomes 0.4–0.5 mm long, along a single line; internodes 15–25 cm long, 1–1.2 mm diam. "*Stipules*" ovate, 5–7 mm long, 5–7 mm wide. *Leaves* with petioles 35–50 mm long, 4–6 colleters at the base of the leaves; leaf blades herbaceous, 60–70 mm long, 30–35 mm wide, ovate, basally lobate, lobes 4–7 mm long, apically acuminate, apiculus 10–12 mm long, adaxially glabrous, abaxially isolatedly covered with flexuous trichomes 0.15–0.2 mm long, concentrated on veins and margins. *Inflorescences*

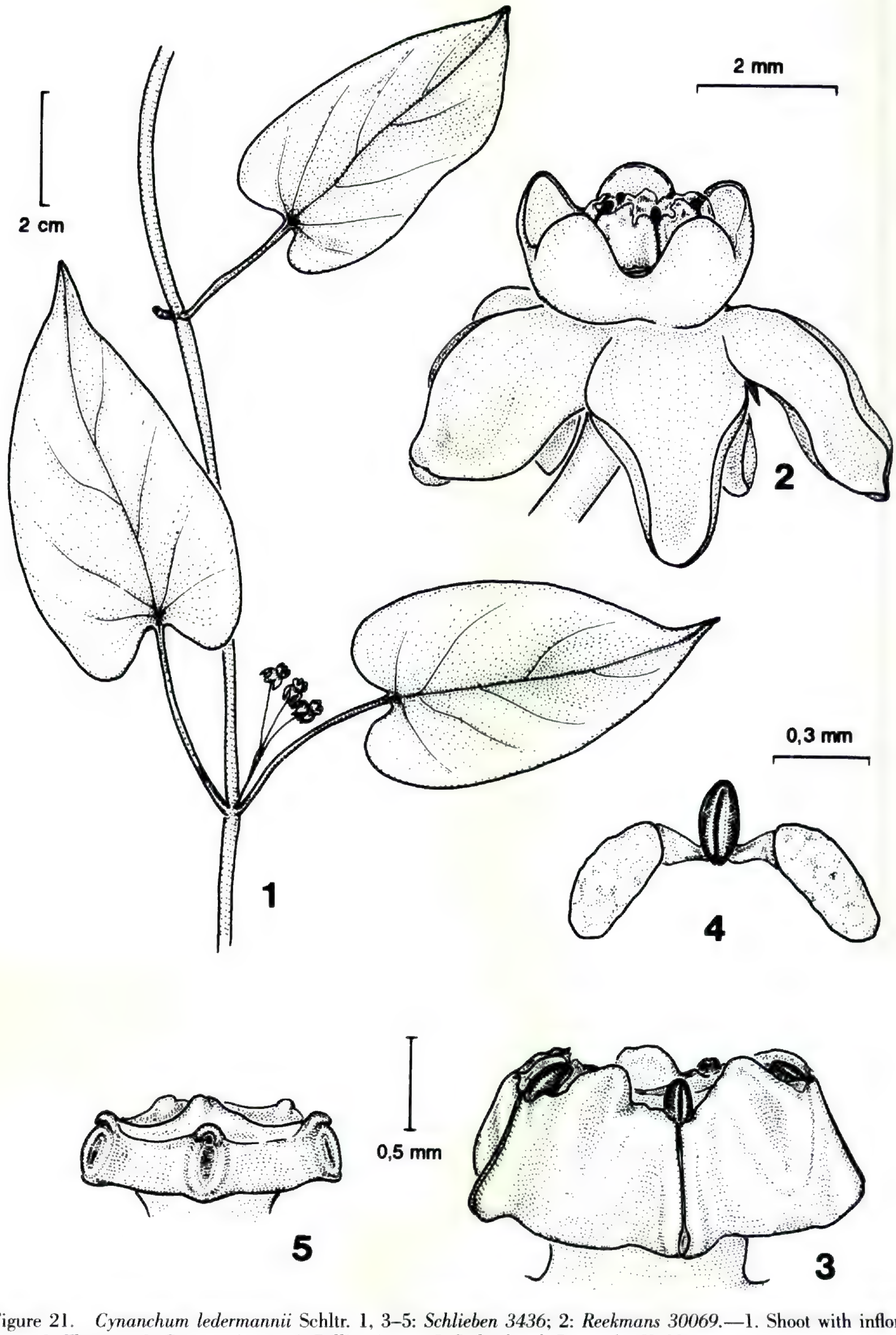


Figure 21. *Cynanchum ledermannii* Schltr. 1, 3–5: *Schlieben 3436*; 2: *Reekmans 30069*.—1. Shoot with inflorescence.—2. Flower.—3. Gynostegium.—4. Pollinarium.—5. Stylar head. Drawn by U. Meve.

sciadioidal, 8–15-flowered; peduncles 35–50 mm long, densely covered with flexuous trichomes 0.25–0.3 mm long, along a single line. *Flowers* with floral bracts 1.6–1.8 mm long, 0.3–0.5 mm wide at the base, elongate-triangular, with trichomes; pedicels 5–7 mm long, densely covered with flexuous trichomes 0.2–0.25 mm long. *Buds* 2–2.5 mm long, 2–2.5 mm diam., globose, with imbricate aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 0.8–1 mm long, 0.5–0.7 mm wide, lanceolate, apically acute. *Corolla* rotate, basally fused; 3.5–4 mm long; lobes 1.7–2 mm wide, decurved, ovate, apically obtuse. *Corona* 1.8–2 mm high, equaling or very slightly exceeding the gynostegium, C(is) consisting of Cs and Ci fused for almost ½ of total corona length, C(is) only Cs differentiated, cyathiform. *Cs* not adnate to the filaments, not appressed to the back of the stamens, without adaxial appendages; *lobes of Cs* laminar, oblong, flat, apically erect, with laterally and apically involute margins. *Gynostegium* 1–1.2 mm high, 1.3–1.5 mm diam., on a bulge 0.5–0.7 mm high. *Stamens* without free filaments; anthers broader than high, trapezoidal, abaxially planar; anther wings 0.7 mm long, convergent, extending beyond the anther proper with stamens forming a basal arch; adjacent anther wings parallel, in the same plane as the anther. Connective appendages ca. 0.5 mm long, 0.5 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.5 mm long, caudicles ca. 0.075 mm long, flattened, straight, horizontal, triangular; pollinia subapically attached to the caudicles, ca. 0.25 mm long, 0.12–0.15 mm wide, ovoid, ovate in cross section. *Stylar head* 0.9–1 mm diam., 0.35–0.4 mm high; upper part 0.1–0.15 mm high, umbonate. *Chromosome number* unknown.

Distribution and habitat. Africa: Burundi, Cameroon, Tanzania (T6), Zaïre; 1700–2000 m; mountain forest. Very rarely collected, but a few collections are probably erroneously hidden among the stacks of *C. schistoglossum* or *C. adalinae* subsp. *mannii*; presumably endangered. Figure 6.

Flowering time. May, October to November.

Additional specimens examined. TANZANIA. **Morogoro:** Uluguru, Nordwestseite, ca. 1100 m, 13 Feb. 1933, *Schlieben 3436* (B). ZAÏRE. Yangambi, 21 July 1950, *Deviet 539* (SRGH).

Comments. In habit, *Cynanchum ledermannii* reminds one strongly of *C. adalinae* subsp. *mannii*; but, as Schlechter remarked in the protologue, the corona of the two species is very distinct. Also, the gynostegium is sessile, the stylar head conspicuously conical in *C. adalinae*, while here, the gynostegium is elevated on a bulge and the stylar head flat to umbonate. The corona reminds one a little of *Pentarrhinum*.

All three syntypes cited by Schlechter (1913) were probably destroyed in B, and isotypes could not be located. As the accurate description allows an exact match of the characters of this species, it is neotypified here.

16. Cynanchum lenewtonii Liede, Kew Bull. 49: 119. 1994. TYPE: Kenya. Northern Frontier: Moyale, 13 Dec. 1952, *Gillett 14031* (holotype, K; isotype, B).

Plants twining, to 2.5 m high, richly basicaulously branched. *Shoots* perennial, semi-succulent, finely striate; obscurely glaucous, sparsely glabrescent with flexuous trichomes 0.3–0.4 mm long; internodes 25–60 cm long, 1.5–2.5 mm diam. Latex present, white (the note "clear juice" on the specimen *Gillett 12964* could not be confirmed by my own field observations). *Leaf scales* papery, 1.2–1.7 mm long, 0.6–0.8 mm wide, ovate, apically acute. *Inflorescences* sciadioidal, 2–6-flowered, 2–4 flowers open at a time, subsessile. *Flowers* with floral bracts 0.5–0.7 mm long, 0.6–0.8 mm wide at the base, triangular, glabrous; pedicels 3–4 mm long, glabrous. *Buds* 2–2.5 mm long, 1.5–2 mm diam., ovoid to cylindrical, with imbricate aestivation. *Calyx* basally fused, abaxial surface glabrous; lobes 0.6–0.7 mm long, 0.4–0.5 mm wide ovate, apically acute. *Corolla* rotate to very widely campanulate, fused between ¼–½ of their length; 2.5–3.5 mm long, abaxially and adaxially greenish yellow; lobes 1–1.2 mm wide, recurved, oblong to triangular, apically obtuse to acute. *Corona* white, cyathiform to campanulate, 2–2.5 mm high, exceeding the gynostegium, partly obscuring it, consisting of Cs and Ci fused for ½ to ¾ of total corona length, both Cs and Ci differentiated, Ci shorter than Cs. *Cs* adnate to the filaments, appressed to the back of the stamens, adaxially with a basal protuberance corresponding to the filament, without adaxial appendages; lobes of Cs filamentose, apically inflexed to erect (when young, they bend over the gynostegium and touch each other in the middle, later they open up); *Ci* laminar, triangular to very narrowly triangular, erect to reflexed; with straight upper margin. *Gynostegium* 1.5–1.6 mm high, 1.3–1.4 mm diam., sessile. *Stamens* with free filaments 0.6–0.7 mm long, broader than high, rectangular, abaxially planar; anther wings 0.18–0.2 mm long, extending along the whole length of the anther, parallel to each other, adjacent anther wings divergent toward

the base, in the same plane as the anther. Connective appendages 0.5–0.6 mm long, 0.65–0.7 mm wide, widely ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.18–0.2 mm long, margins of the corpuscular cleft sinuate; caudicles 0.1–0.12 mm long, flattened, straight, horizontal, not thickened at the insertion of the pollinium; pollinia laterally attached to the caudicles, 0.25–0.3 mm long, 0.13–0.15 mm wide, ovoid, ovate to round in cross section. *Stylar head* 0.6–0.65 mm diam., 0.45–0.5 mm high; upper part 0.17–0.2 mm high, flat to depressed-conical. *Follicles* one, occasionally two, per flower, erect, 65–70 mm long, obclavate, wingless. *Seeds* unknown. *Chromosome number*: $2n = 22$ (voucher: *Liede & Newton 3161*, MSUN).

Distribution. Africa: Ethiopia (Bale), Kenya (K1). Figure 18.

Comments. *Cynanchum lenewtonii* is closely related to *C. gerrardii*, but is easily recognized by its long staminal corona parts closing over the gynostegium in young flowers.

Further comments, citation of specimens, and illustration are provided in Liede (1994).

17. Cynanchum longipes N. E. Brown, Bull. Misc. Inform., Kew 1897: 273. 1897. TYPE: Nigeria. Lagos: Papalayito, 1895, *Millen 48* (holotype, K). Figure 22.

Plants ascending, twining, 5–8 m high, richly and irregularly branched. *Shoots* perennial, herbaceous, sparsely covered with erect trichomes 0.7–0.9 mm long, along a single line; internodes 10–20 cm long, 1.5–1.7 mm diam. "*Stipules*" ovate, acute, 10–15 mm long, 8–12 mm wide. *Leaves* with petioles 15–100 mm long; leaf blades herbaceous, 60–115 mm long, 23–65 mm wide, ovate, basally lobate, lobes 10–15 mm long, with 9–11 colleters in the adaxial sinus, leaves apically acuminate, apiculus 8–12 mm long, adaxially and abaxially glabrous. *Inflorescences* bostrychoid, 5–9-flowered, all flowers open at a time; rachis 2–7 mm long; peduncles 5–7 mm long, sparsely covered with flexuous trichomes 0.15–0.2 mm long, along a single line. *Flowers* with floral bracts 1–1.2 mm long, 0.2–0.4 mm wide at the base, triangular; pedicels 10–20 mm long, densely covered with flexuous trichomes 0.15–0.25 mm long. *Buds* 5–6 mm long, 3.5–4 mm diam., conical, with imbricate aestivation. *Calyx* basally fused, ciliate; lobes 1.4–1.5 mm long, 0.9–1 mm wide, ovate, apically acute. *Corolla* rotate, basally fused; 6–8 mm long, abaxially greenish yellow, adaxially yellow; lobes 2–2.5 mm wide, horizontal, oblong, apically obtuse. *Corona* purplish red, 5–6 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* basally just adnate to the filaments, without adaxial appendages; lobes of Cs laminar, triangular or trifid (with two short side teeth), apically erect. *Lobes of Ci* laminar, triangular, erect. *Gynostegium* 0.35–0.4 mm high, 0.45–0.5 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, pentagonal, abaxially convex; anther wings 0.24–0.26 mm long, parallel to each other, extending along the whole length of the anther, adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.15–0.2 mm long, 0.14–0.16 mm wide, triangular, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.35–0.37 mm long, between 1.5 times and twice as long as broad, rhomboid; caudicles 0.2 mm long, flattened, straight, declinate, triangular; pollinia subapically attached to the caudicles, 0.66–0.68 mm long, 0.25 mm wide, oblongoid, round in cross section. *Stylar head* 0.28–0.3 mm diam., 0.6–0.8 mm high; upper part 0.3–0.45 mm high, flat to depressed-conical to conical. *Follicles* one per flower, pendulous, ca. 90 mm long, 7.5 mm diam., fusiform, apically acute, but not beaked, keeled, medium brown. *Seeds* and *chromosome number* unknown.

Distribution and habitat. Africa: Cameroon, Gabon, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Nigeria, Sierra Leone, Uganda, Zaïre; 250–1300 m; forest, gallery forest, forest clearings and plantations. Not frequent, but very widespread. Figure 8.

Flowering time. (May–)July to November.

Selected specimens examined. CAMEROON. Southwest, around Kumba, 150 m, 16 May 1984, *Thomas 3483* (MO); Bitye near River Ja, Sep. 1922, *Bates 1856* (K). GABON. La Waka, Oubangui-Chari A.E.F., Glatemazé, 20 km NE Boubani, 1927, *Le Testu 2285* (BM); Mbaïki, Boukoko, 5 July 1948, *Le Testu 1027* (BM); Woleu-Ntem, Minvoul, 15 Aug. 1923, *Le Testu 234* (BM). GUINEA. Fá, 10 Sep. 1962, *Guerra 3839* (K); Kinsan, Kindia, July 1937, *Jacques-Félix 1810* (K, P). GUINEA-BISSAU. Bafatá, entre Geba e Mato de Cao, 15 Sep. 1955, *Junta de Investgações coloniais 3370* (K). IVORY COAST. Bouaké, route de Sakasso, km 12, 250 m, 9 Aug. 1963, *Garnier & Bouaké 95* (K); Boukoka, 2 Aug. 1947, *Tiss 102* (G). LIBERIA. Bong, Gbanga, 1926, *Linder 653* (K); Nimba, Nimba Reserve, Mount Bele Rd., 500 m, 10 Sep. 1964, *Adames 512* (K). NIGERIA. West, Ife, Shasha forest Reserve, on track 26, 20 Sep. 1973, *Latilo s.n.* (*67538 FHI*, K). SIERRA LEONE. Mamaba, 2 Nov. 1914, *Thomas 4553* (K); Njala, 8 Oct. 1949, *Deighton 5188* (B, K); Ronietta, 250 m, 17

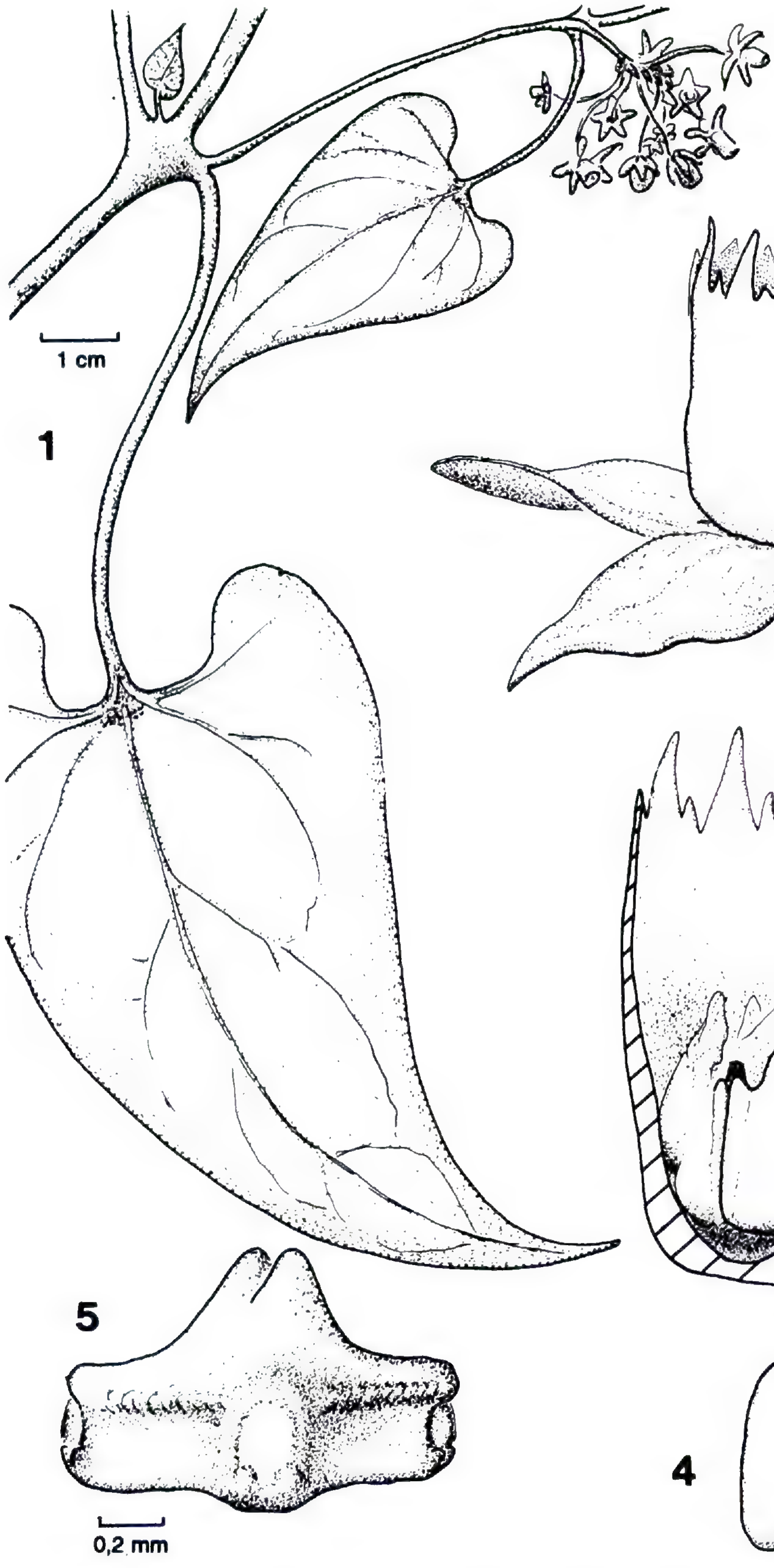


Figure 22. *Cynanchum longipes* N. E. Br. 1: *Junta de investigações coloniais 3311*; 2–5: *Adames 512*. —1. Habit with inflorescence.—2. Flower.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head. Drawn by Jim Conrad.

Nov. 1914, *Thomas 5377* (K). ZAÏRE. Lilando, 15 Aug. 1938, *Louis 10843* (K).

Comments. *Cynanchum longipes* is a species of uncertain affinities, the red corona resembling the Malagasy *C. papillatum* alliance, but with the habit of a rather unspecialized species.

This species is illustrated in Adam (1975: 971, pl. 506).

18. Cynanchum meyeri (Decaisne) Schlechter, Bot. Jahrb. Syst. 20, Beibl. 51: 2. 1895. *Cynoctonum meyeri* Decne. in Candolle, Prodr. 8: 531. 1844. (nom. superfl. when published, based on *S. ovatum* E. Mey.). *Vincetoxicum meyeri* (Decne.) Kuntze, Revis. Gen. Pl. 2: 424. 1891. *Sarcostemma ovatum* E. Mey., Comm. Pl. Afr. Austr.: 216. 1838. *Cynanchum ovatum* (E. Mey.) Druce, Bot. Soc. Exch. Club Brit. Isles 4: 618. 1917, non *Cynanchum ovatum* Thunb., Observ. Cynanch.: 6. 1821 (= *Leptadenia*). TYPE: Namibia. Garip, in collibus ad ostium fluminis, < 200 m, Oct., *Drège s.n.* (holotype, SAM sub SAM *18556*; isotype, MO sub MO *2760941*).

Metaplexis mucronata Spreng., Neue Entdeck. Pflanzenk. 1: 269. 1820. *Cynanchum mucronatum* (Spreng.) N. E. Br. in Dyer, Fl. Cap. 4(1): 745. 1908, non *Cynanchum mucronatum* Andrews, Bot. Repos. 8: t. 515. 1808. TYPE: not known.

Cynanchum pearsonii N. E. Br., Bull. Misc. Inform., Kew 1914: 18. 1914. TYPE: Namibia. Great Namaqualand, Lüderitz, N of Rotkuppe Station, 23 Feb. 1909, *Pearson 4466* (holotype, K; isotype, BOL).

Plants erect, 20–40 cm high, richly branched. *Shoots* perennial, 15–30 cm long, 4 mm diam., obscurely glaucous, woody with grayish bark, isolatedly to densely covered with appressed trichomes 0.2–0.25 mm long, glabrescent. "*Stipules*" ovate, 5 mm long, 3 mm wide. *Leaves* with petioles 1–3.5 mm long; leaf blades coriaceous, 7–20 mm long, 4–10 mm wide, ovate, basally rounded, without colleters, apically acute, or obtuse and apiculate, adaxially isolatedly covered with appressed trichomes 0.1–0.15 mm long, evenly distributed over the whole surface; abaxially glabrous. *Inflorescences* bostrychoid, 6–13-flowered, 2–8 flowers open at a time; rachis 1–2 mm long; peduncles 1–3 mm long, densely covered with appressed trichomes 0.15–0.2 mm long. *Flowers* with floral bracts 0.6–0.8 mm long, 0.7–0.9 mm wide at the base, triangular, with trichomes; pedicels 2–4 mm long, densely covered with appressed trichomes 0.15–0.2 mm long. *Buds* 0.8–1.2 mm long, 0.7–0.9 mm diam., conical; aestivation imbricate. *Calyx* basally fused, abaxially with trichomes; lobes 1–1.2 mm long, 0.5–0.6 mm wide, ovate, apically obtuse to acute. *Corolla* rotate to subglobose, fused for about ¼ of their length, 1.5–2 mm long, abaxially glabrous, or with isolated trichomes, green to white; adaxially glabrous, green to white; lobes 0.5–1 mm wide, ovate, apically obtuse to acute, patent to recurved. *Corona* white, cyathiform, 1–1.5 mm high, exceeding the gynostegium but not obscuring it; *C(is)* consisting of Cs and Ci for about half of total height, only Cs differentiated in shape. *Cs* without adaxial appendages; lobes of Cs flat, triangular, erect, with straight margins. *Gynostegium* 0.7–0.75 mm high, 0.9–0.95 mm diam., sessile. *Stamens* with free filaments 0.2–0.25 mm long, anthers broader than high, trapezoidal, abaxially convex; anther wings 0.25–0.26 mm long, convergent, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.35–0.4 mm long, 0.22–0.25 mm wide, ovate, narrower than the stamens, erect. *Pollinarium*: corpusculum 0.12–0.13 mm long; caudicles 0.04–0.05 mm long, cylindrical, s-shaped, concave-convex; pollinia apically attached to the caudicles, 0.15–0.17 mm long, 0.05–0.06 mm wide, pyriform, elliptical in cross section. *Stylar head* 0.6–0.65 mm diam., 0.5–0.55 mm high; upper part 0.25–0.3 mm high, conical to depressed-conical. *Follicles* 30–35 mm long, 4–6 mm wide, obclavate, round in cross section, apically strongly beaked, gray, smooth, with isolated hairs. *Seeds* 4.5–5.5 mm long, 2.5–3.5 mm wide, pyriform, dark brown, seta and aseta side tuberculate, marginally wingless, entire; coma 15 mm long. *Chromosome number* unknown.

Distribution. Africa: Namibia. Lüderitz; 0–200 m; flats and slopes; sand and rock crevices; frequently on granite.

Comments. Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

19. Cynanchum mossambicense K. Schumann in Engler, Pflanzenw. Ost-Afrikas C: 323. 1895. TYPE: Mozambique. Zambesia: Quillimane, *Stuhlmann 843* (holotype, B presumably destroyed; lectotype, designated here, K)

Cynanchum complexum N. E. Br., Bull. Misc. Inform., Kew 1895: 256, 337. 1895. TYPE: Mozambique. Mapanga, Oct. 1887, *Scott s.n.* (lectotype, designated here, K).

Plants twining, richly branched. *Shoots* perennial, 1–1.5 mm diam., herbaceous, sparsely to densely covered with erect trichomes 0.5 mm long.

"*Stipules*" absent. *Leaves* with petioles 15–20 mm long; leaf blades herbaceous, 25–50 mm long, 15–30 mm wide, ovate, basally cordate with 2 colleters in the adaxial sinus, apically acute and apiculate, apiculus 1–2 mm long, adaxially and abaxially nearly glabrous. *Inflorescences* sciadioidal, 5–12-flowered, all flowers open at a time; peduncles 8–12 mm long, glabrous, or sparsely covered with appressed trichomes 0.4 mm long. *Flowers* with floral bracts 1–1.2 mm long, 0.5–0.6 mm wide at the base, ovate, with trichomes; pedicels 5–7 mm long, glabrous. *Buds* 5.5–7 mm long, ca. 3.5 mm diam., conical to elongate-conical; aestivation slightly contorted. *Calyx* basally fused, abaxially glabrous; lobes 1.2–1.5 mm long, 0.5–0.7 mm wide, ovate, apically acute. *Corolla* rotate, fused at the base, 6–7 mm long; abaxially and adaxially glabrous, white; lobes 1.5–2 mm wide, spreading to recurved, oblong, apically obtuse, twisted. *Corona* white, tubular, 5–6 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for little more than half of total corona length; Cs and Ci differentiated in shape; Ci as long as Cs, thinner than Cs. *Cs* appressed to the back of the stamens, with adaxial appendages; lobes of Cs flat, triangular, erect, with laterally involute margins; adaxial appendages shorter than Cs, erect, liguliform. *Lobes of Ci* basally flat, elongatedly triangular, apically filamentose, twisted, erect, with laterally involute margins. *Gynostegium* 1.8–1.9 mm high, 1.8–1.9 mm diam., sessile. *Stamens* without free filaments; anthers higher than broad, trapezoid, abaxially planar; anther wings convergent, 0.9–0.95 mm long, extending beyond the anther proper with stamens basally slightly arched; adjacent anther wings parallel, centrifugal, outer guide rail smooth. Connective appendages 0.75–0.8 mm long, 0.47–0.5 mm wide, triangular, equaling the stamen in width, slightly inflexed. *Pollinarium*: corpusculum 0.3–0.35 mm long; margins of the corpuscular cleft sinuate; caudicles 0.05–0.06 mm long, flattened, straight, horizontal to declinate, triangular; pollinia subapically attached to the caudicles, 0.42–0.45 mm long, 0.2–0.23 mm wide, ovoid to oblong, ovate in cross section. *Stylar head* 0.8–0.85 mm diam., 1–1.1 mm high; upper part 0.4–0.45 mm high, bifurcate. *Follicles* 55–70 mm long, 4–5 mm diam., obclavate, obtusely deltate in cross section, apically shortly beaked, keeled, medium brown, longitudinally grooved, glabrous. *Seeds* 5.5–6 mm long, 4 mm wide, ovate, medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.3–0.35 mm wide wing with entire margin; coma 15–20 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Mozambique, South Africa (Transvaal), Swaziland, Zimbabwe; 0–1000 m; on sand and over rocks, coastal dune scrub, riverine forest. Not frequent, but probably not endangered. Figure 4.

Flowering time. March to October.

Selected specimens examined. MOZAMBIQUE. Inhambane, 0 m, 14 Oct. 1906, *Johnson s.n.* (K); Manica, near Gondola, 1000 m, 16 June 1957, *Pole Evans 5226* (K); Sofala, Chiloane, Oct. 1887, *Scott s.n.* (K); Zambesia, Quelimane (20 mi. N of), 20 Aug. 1962, *Wild 5882* (K, MO, SRGH). SOUTH AFRICA. **Transvaal:** Acornhoek, between Skukuza and Pretorius Kop, on banks of Sabi near Hippo Pool, Oct. 1931, *Letty 91* (PRE, SRGH). SWAZILAND. Stegi, Mbuluzi River, near Ranches, ca. 330 m, 25 July 1958, *Compton 27923* (NBG, PRE). ZIMBABWE. Chiredzi, Gona-re-zhou, 2 km from Chipindas Pools on N bank of Lundi River, on edge of research Officer's garden, 28 May 1971, *Grosvenor 554* (K, SRGH); Darwin, near upper reaches of Nyatandi river, 900 m, 27 Jan. 1960, *Phipps 2426* (K, SRGH); Ndanga, Sabi-Lundi-Junction, Chitsis Kraal, 270 m, 6 June 1950, *Wild 3393* (K, SRGH).

Comments. *Cynanchum mossambicense*, a species restricted to a rather small area in southeastern Africa, is probably the closest African relative of *C. acutum*.

Lectotypification of *C. mossambicense* is necessary because the original material was destroyed in B. The isotype in K is chosen as lectotype. N. E. Brown cited two specimens (*Kirk s.n.* and *Scott s.n.*, both K) as syntypes for *C. complexum*. The better specimen, *Scott s.n.*, is chosen as lectotype.

Illustration and additional information on southern African material are provided in Liede (1993).

20. Cynanchum natalitium Schlechter, Bot. Jahrb. Syst. 18, Beibl. 45: 32. 1894. TYPE: South Africa. Natal: Durban, 14 Aug. 1893, *Schlechter 3082* (lectotype, designated by Liede (1993), BOL; isolectotype, GRA).

Plants twining, to 30 cm high, richly branched, sarmentose, adventitious roots formed along the whole lower surface of the runner; subterranean organs consisting only of fibrous roots. *Shoots* perennial, 30–150 cm long, 1–2 mm diam., herbaceous, isolatedly glabrescent with appressed trichomes 0.25–0.3 mm long; in old plants basally corky, then bark yellowish. "*Stipules*" ovate, 5–6 mm long, 3–4 mm wide. *Leaves* with petioles 7–25 mm long; leaf blades fleshy, 20–50 mm long, 15–35 mm wide, ovate to orbicular, or obovate, basally rounded, or cuneate with 1 colleter adaxially, apically obtuse and acuminate, acumen 0.5–1.5 mm long, glabrous, or isolatedly covered with appressed trichomes 0.35–0.5 mm long, evenly distributed over the whole surface. *Inflorescences* sciadioidal (some-

times two sciadioids in dichasial arrangement), 6–16-flowered, 6–12 flowers open at a time; peduncles 5–15 mm long, glabrous, or isolatedly covered with appressed trichomes 0.25–0.35 mm long. *Flowers* sweetly scented; floral bracts 1–1.5 mm long, 0.5–1 mm wide at the base, ovate, with trichomes; pedicels 5–10 mm long, isolatedly covered with appressed trichomes 0.3–0.35 mm long. *Buds* 4–5 mm long, 2–3 mm diam., elongated-conical; aestivation imbricate. *Calyx* basally fused, abaxially with trichomes; lobes 0.8–1.2 mm long, 0.6–1 mm wide, triangular, apically acute. *Corolla* rotate, basally fused 3.5–5 mm long, abaxially and adaxially glabrous, dull green to brown; lobes 1.5–2 mm wide, spreading to patent, oblong, apically obtuse. *Corona* white, urceolate, 3.5–4 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci completely fused, upper margin deeply 5-crenate, margins of sinuses recurved; *Cs* without adaxial appendages. *Gynostegium* 0.8–1.2 mm high, 1.5–1.8 mm diam., atop a stipe 1–1.5 mm long. *Stamens* without free filaments; anthers about as high as broad, trapezoidal, abaxially convex; anther wings 0.23–0.25 mm long, not extending along the whole length of the anther, adjacent anther wings parallel, basally widened, in the same plane as the anther. Connective appendages 0.5–0.55 mm long, 0.4–0.45 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.3–0.32 mm long; margins of the corpuscular cleft divergent toward the base; caudicles 0.1–0.12 mm long, flattened, straight, declinate, triangular; pollinia subapically attached to the caudicles, 0.4–0.45 mm long, 0.15–0.17 mm wide, clavate, elliptical in cross section. *Stylar head* 0.5–0.55 mm diam., 0.3–0.35 mm high, upper part ca. 0.1 mm high, flat. *Follicles* 40–45 mm long, 5–8 mm wide, obclavate, obtusely deltate in cross section, apically strongly beaked, keeled to winged with 0.5–1 mm broad wing, medium brown, longitudinally grooved, with isolated trichomes. *Seeds* 5.5–6.0 mm long, 3–3.5 mm wide, ovate, light to medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with indistinct, 0.5 mm wide wing with entire margin; coma 15–17 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: South Africa (Cape Province, Natal); 0–60 m; on littoral dunes, dune forest; full sun to light shade.

Comments. Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

21. Cynanchum obtusifolium Linnaeus f., Suppl. Pl. 169. 1784. *Vincetoxicum obtusifolium* (L. f.) Kuntze, Revis. Gen. Pl. 3, 2: 200. 1898. TYPE: *Thunberg s.n.* (holotype, *UPS 6311*, UPS; seen on IDC microfiche).

Cynoctonum brownii Meisn., J. Bot. 2: 546 ("446"). 1843. Nom. superfl. when published, substitute name for *Cynanchum obtusifolium* L.f.

Plants twining, 2–3 m high, richly branched; subterranean organs consisting only of fibrous roots. *Shoots* perennial, 50–200 cm long, 1–1.5 mm diam., herbaceous, glabrous, or sparsely to densely covered with erect trichomes 0.4–0.7 mm long, basally woody with yellowish bark. "*Stipules*" ovate, almost round, 5–7 mm long, 6–8 mm wide. *Leaves* with petioles 5–15 mm long; leaf blades herbaceous to thinly coriaceous, 20–40 mm long, 15–40 mm wide, ovate to elliptic, basally rounded to subtruncate, or cordate, with 2–4 colleters in the adaxial sinus, apically obtuse and acuminate, or obcordate and acuminate, marginally entire or crenulate, adaxially and abaxially glabrous, or with a sparse indumentum concentrated on veins and margins; trichomes appressed, 0.3–0.45 mm long. *Inflorescences* bostrychoid, 8–15-flowered, 3–6 flowers open at a time; rachis 1–3 mm long; peduncles 3–5 mm long, densely covered with erect trichomes 0.5–0.7 mm long. *Flowers* sweetly scented; floral bracts 1–2.5 mm long, 0.5–0.7 mm wide at the base, ovate, with trichomes; pedicels 3.5–6 mm long, densely covered with appressed trichomes 0.4–0.7 mm long. *Buds* 4–5 mm long, 2–3 mm diam., elongated-conical; aestivation imbricate. *Calyx* basally fused, abaxially with trichomes; lobes 1.5–2 mm long, 0.8–1.2 mm wide, ovate, apically acute to acuminate. *Corolla* rotate, fused at the base, 3–4 mm long, abaxially glabrous, green, adaxially with verrucose trichomes, green; lobes 1–1.5 mm wide, patent, ovate to oblong, apically obtuse. *Corona* white, cyathiform, 2–2.5 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci fused between for about ½ of total corona length; Cs and Ci differentiated in shape, Ci shorter than Cs, dorsally connate to Cs. *Cs* without adaxial appendages; lobes of Cs flat, trifid (the two lateral teeth much smaller than the middle one), inflexed, with laterally involute margins. *Lobes of Ci* flat, rectangular, erect, with straight, emarginate margins. *Gynostegium* 1.5–2 mm high, 1.5–2 mm diam., sessile. *Stamens* without free filaments, anthers about as broad as high, trapezoidal, abaxially convex; anther wings 0.5–0.55 mm long, extending beyond the anther proper, which does not form a basal arch; adjacent anther

wings parallel, basally widened. Connective appendages 0.25–0.3 mm long, 0.5–0.55 mm wide, depressed ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.25–0.27 mm long; margins of the corpuscular cleft sinuate; caudicles 0.12–0.13 mm long, flattened, straight, declinate, triangular; pollinia subapically attached to the caudicles, 0.375–0.4 mm long, 0.16–0.18 mm wide, ovoid. *Stylar head* 1–1.1 mm diam., 0.7–0.75 mm high; upper part 0.5–0.55 mm high, upper part depressed-conical and umbonate. *Follicles* 40–50 mm long, 10–12 mm wide, obclavate, obtusely deltate in cross section, apically obtuse, keeled, medium to dark brown, longitudinally grooved, sparsely to densely covered with trichomes. *Seeds* 6–7 mm long, 3.5–4 mm wide, pyriform, dark brown, seta and aseta side sculptured with longitudinal ridges and papillose, marginally with 1.0–1.1-mm-wide wing with entire margin; coma 30 mm long. *Chromosome number*: $2n = 22$ (voucher: *Liede 2924*, MSUN).

Distribution and habitat. Africa: Mozambique, South Africa (Cape Province, Natal); 0–250 m; dunes; mostly on sand; dune scrub and coastal vegetation; frequently in disturbed habitats; full sun to partial shade.

Comments. *Periploca africana* L. var. ß L. [Sp. Pl. ed. 1: 211, 1753, illustrated with Burman, Rar. Afr. Pl.: p. 34, t. 14, fig. 2. 1738] also represents this taxon.

Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

22. Cynanchum orangeanum (Schlechter) N. E. Brown in Dyer, Fl. Cap. 4(1): 745. 1908. *Flanagania orangeana* Schltr., Bot. Jahrb. Syst. 18, Beibl. 45: 10. 1894. TYPE: South Africa. Orange Free State: Colesberg, Orange River near Bethulie, 1330 m, Dec. 1892, *Flanagan 1502* (lectotype, designated by Liede (1993), SAM; isolectotype, BOL).

Plants erect, 10–20 cm high, basally sparsely branched; subterranean organs rhizomatous, rhizome 5–7 mm diam. *Shoots* 15–20 cm long, 1–1.5 mm diam., herbaceous, densely to sparsely covered with erect trichomes 0.25–0.27 mm long, basally woody with grayish bark. "*Stipules*" absent. *Leaves* sessile; leaf blades herbaceous, 30–50 mm long, 0.7–1.5 mm wide, linear, basally decurrent, without colleters, apically acute, or obtuse, marginally straight and thickened, adaxially and abaxially glabrous, or isolatedly covered with appressed trichomes 0.15–0.2 mm long, restricted to the veins and margins. *Inflorescences* sciadioidal, 1–5-flowered, all flowers open at a time (one extraordinary umbel seen with 16 flowers, *Hardy 6583*, PRE); peduncles 0–5 mm long, isolatedly to sparsely covered with erect trichomes 0.2–0.25 mm long. *Flowers* with floral bracts 1–1.5 mm long, 0.3–0.5 mm wide at the base, linear, with trichomes; pedicels 3–7 mm long, sparsely to densely covered with appressed trichomes 0.25–0.3 mm long. *Buds* 2.5–4 mm long, 2–3 mm diam., depressed-conical; aestivation imbricate. *Calyx* basally fused, abaxially with trichomes (prominently so along the midrib); lobes 2–2.5 mm long, 0.8–1.2 mm wide, ovate, apically acute. *Corolla* rotate, basally fused, 4–6 mm long, abaxially glabrous (or with a few isolated trichomes), brown, adaxially glabrous, brown; lobes 1.5–2 mm wide, incurved, ovate to lanceolate, apically acute, margins revolute. *Corona* white, cyathiform, 4–5 mm high, shorter than the gynostegium; C(is) consisting of Cs and Ci fused for about ½ of total height, both Cs and Ci differentiated in shape, Ci as long as Cs. *Cs* appressed to the back of the stamens; lobes of Cs flat, oblong, reflexed, without adaxial appendages. *Lobes of Ci* filamentous, reflexed, with straight margins. *Gynostegium* 1.5–2 mm high, 1.5–2 mm diam., sessile. *Stamens* without free filaments; anthers broader than high, rectangular, abaxially convex; anther wings 0.4–0.5 mm long, convergent, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.5–0.55 mm long, 0.65–0.7 mm wide, widely ovate, narrower than the stamen, erect. *Pollinarium*: corpusculum 0.2–0.25 mm long; margins of the corpuscular cleft parallel; caudicles 0.15–0.175 mm long, cylindrical, s-shaped, concave-convex, thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, 0.3–0.35 mm long, 0.12–0.15 mm wide, ovoid, round in cross section. *Stylar head* 0.8–0.85 mm diam., 0.9–1 mm high; upper part 0.7–0.75 mm high, capitate. *Follicles* 40–70 mm long, 4–7 mm wide, fusiform, round in cross section, apically strongly beaked, light brown, smooth, glabrous. *Seeds* 5–6 mm long, 3–3.5 mm wide, ovate, dark brown; seta and aseta side tuberculate, marginally with 0.6-mm-wide wing with entire margin; coma 15–20 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Botswana, Namibia, South Africa (Cape Province, Orange Free State), Zimbabwe; 1000–1500 m; on flats, in sand, frequently red Kalahari sand, between rocks, short grassland; full sun. Figure 23.

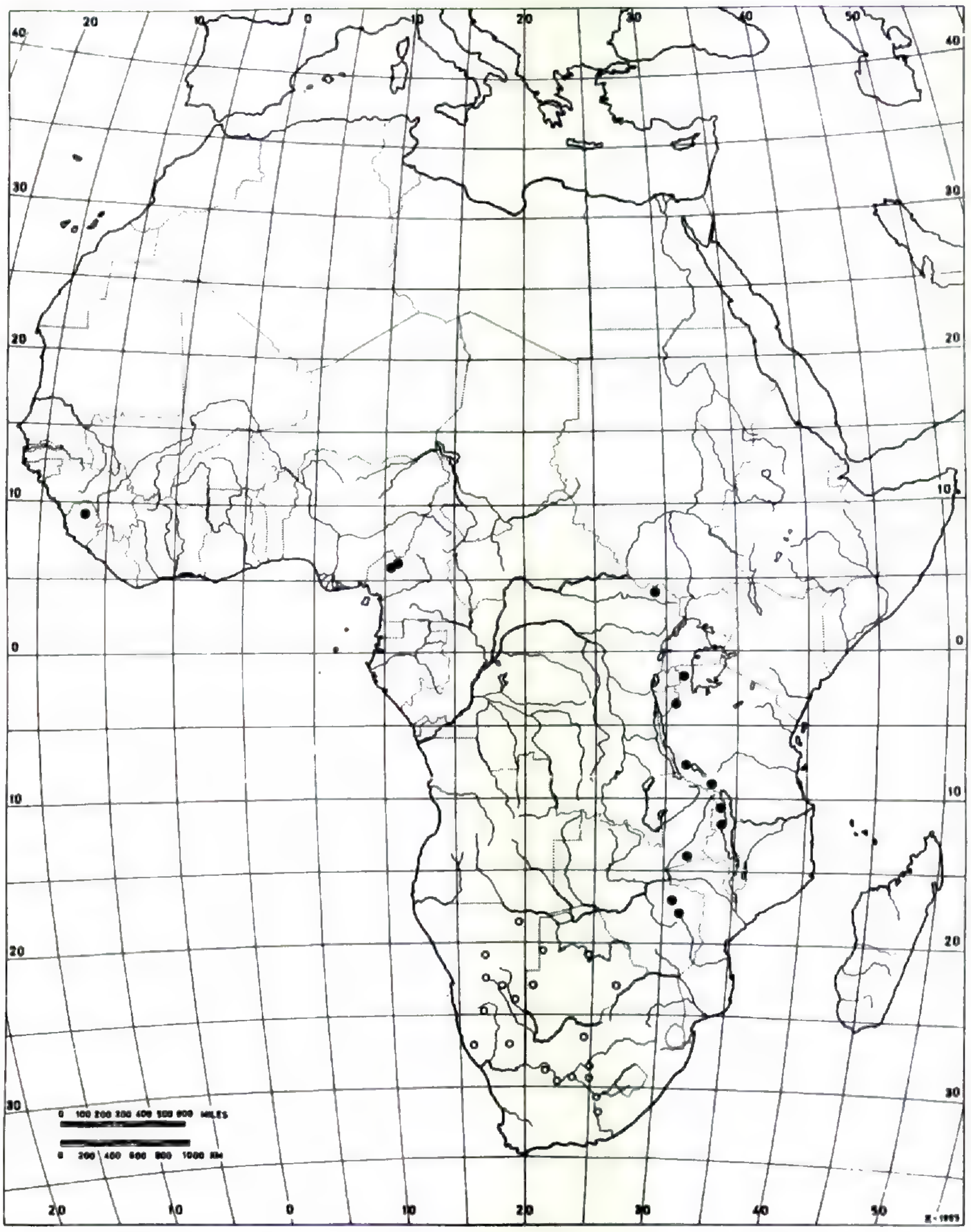


Figure 23. Known distribution of *C. orangeanum* (open circles) and *C. praecox* (dots).

Comments. *Cynanchum orangeanum* is closely related to *C. praecox*, but is otherwise isolated among African *Cynanchum*.

Further details, illustration, and citation of specimens are provided in Liede (1993).

23. Cynanchum polyanthum K. Schumann in Engler & Prantl, Nat. Pflanzenfam. 4(2): 253. 1895. TYPE: "Im Land der Monbuttu bei Manza," *Schweinfurth 3345* (holotype, B presumably destroyed; lectotype, designated here, K). Figure 24.

Vincetoxicum polyanthum K. Schum., Bot. Jahrb. Syst. 17: 136. 1893, non *Vincetoxicum polyanthum* Kuntze, Revis. Gen. Pl. 2: 424. 1891, replacement name for *Tylophora floribunda* Miq.

Cynanchum obscurum K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4(2): 253. 1895. TYPE: Angola. Cuanza Norte, Golungo Alto, Ad dumeta in Sobato de Mussengue, Jan. 1870, *Welwitsch 4222* (holotype, K; isotype, BM).

Cynanchum welwitschii Schltr. & Rendle, J. Bot. 34: 99. 1896. Nom. illeg., because the protologue included a reference to the holotype of *Cynanchum obscurum* K. Schum. (Art. 52.1 ICBN, see Greuter et al., 1994).

Periploca batesii Wernham, J. Bot. 54: 228. 1916. TYPE: Cameroon. Bitye, 2 Dec. 1914, *Bates 643* (holotype, BM).

Plants ascending, twining, 2.5–3 m high, sparsely and irregularly branched; subterranean organs woody rootstocks. *Shoots* perennial, herbaceous, sparsely covered with flexuous trichomes 0.5–0.6 mm long, along two lines; internodes 7–10 cm long, 0.5–2 mm diam. "*Stipules*" absent. *Leaves* with petioles 15–50 mm long; leaf blades herbaceous, 55–100 mm long, 35–55 mm wide, ovate, basally lobate, lobes 10–15 mm long, with 3–5 colleters in the adaxial sinus, apically acuminate, acumen 1–2

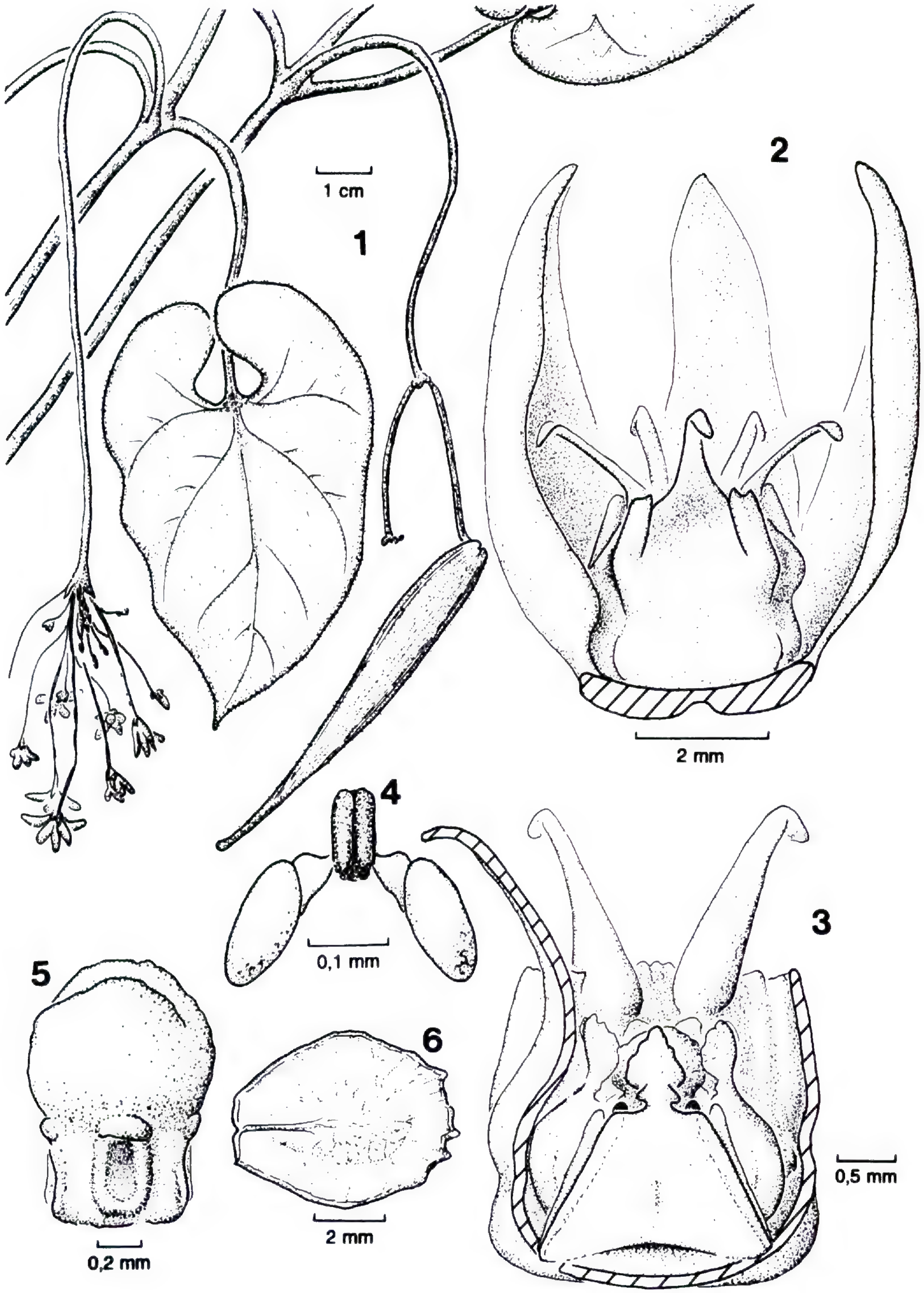


Figure 24. *Cynanchum polyanthum* K. Schum.—1. Habit with inflorescence (*De Witte 11112*) and fruit (*Gossweiler 4866*). 2–5: *De Witte 11112*.—2. Flower and corona, two corolla lobes removed.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head.—6. Seed, seta side (*Synnott 688*). Drawn by Jim Conrad.

mm long, adaxially isolatedly covered with flexuous trichomes 0.55–0.6 mm long, restricted to veins and margins, abaxially sparsely covered with flexuous trichomes 0.4–0.5 mm long. *Inflorescences* bostrychoid to sciadioidal, 8–15-flowered, 6–10 flowers open at a time; rachis to 7 mm long; peduncles 35–75 mm long, sparsely covered with appressed trichomes 0.5–0.6 mm long. *Flowers* with floral bracts 1.2–1.4 mm long, 0.4–0.8 mm wide at the base, ovate, with trichomes; pedicels 12–35 mm long, densely covered with erect trichomes 0.4–0.5 mm long. *Buds* 5–6 mm long, 2.5–3 mm diam., conical, basally with imbricate, apically with contorted aestivation. *Calyx* basally fused, abaxial surface with trichomes; lobes 0.8–1 mm long, 0.6–0.7 mm wide, ovate, apically acute. *Corolla* rotate, basally fused; 7–9 mm long, abaxially greenish yellow, adaxially greenish yellow to purple, with a very few isolated trichomes at the sinuses; lobes 1.5–2 mm wide, horizontal, lanceolate to oblong, apically obtuse. *Corona* white, 6–7.5 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for more than ½ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, elongated-triangular, apically erect. *Lobes of Ci* laminar, bifid, producing a pronounced convex fold along the upper half of corona length, reflexed. *Gynostegium* 2–2.5 mm high, 2–2.5 mm diam., sessile. *Stamens* without free filaments; anthers broader than high, trapezoidal, abaxially planar; anther wings 2 mm long, convergent, extending along the whole length of the anther, adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.5–0.6 mm long, 0.5–0.6 mm wide, obovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.3–0.35 mm long, ovoid; caudicles 0.1 mm long, flattened, straight, declinate, trapezoid; pollinia subapically attached to the caudicles, 0.3–0.35 mm long, 0.12 mm wide, oblongoid, ovate in cross section. *Stylar head* 0.7–0.85 mm diam., 0.7–0.85 mm high; upper part 0.4–0.5 mm high, capitate. *Follicles* usually one per flower, pendulous, 80–90 mm long, 7.5–8 mm diam., obclavate, obtusely deltate in cross section, apically strongly beaked, keeled, with isolated indumentum. *Seeds* 5.5–6 mm long, 4.3–4.5 mm wide, ovate, medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with 1-mm-wide wing with dentate margin; coma 12–15 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Angola, Cameroon, Gabon, Uganda (U3, U4), Zaïre; 1200–1600 m, moist grassland, forest margins, thickets. Very widespread, but not frequent. Figure 16.

Flowering time. September to May.

Vernacular name. Molo-Busyo (Lissango).

Selected specimens examined. ANGOLA. Cuanza Norte, Golungo alto, Nov. 1878, *Welwitsch 4200* (G, K). CAMEROON. Yaunde, *Zenker 223* (K). GABON. Mbaïki, Boukoko 27 June 1949, *Le Testu 1510* (BM). UGANDA. Buganda, Mengo, Mutingo, edge of Lake Victoria, a few miles from Kampala, 1250 m, Dec. 1935, *Chandler 1496* (K); Masaka, 4 mi. from Masaka on rd. to Bukakata, 1150 m, 11 Oct. 1953, *Drummond & Hemsley 4736* (K); Eastern, Busoga, Bugabula, Musumu swamp at crossing of Jinja-Kamuli rd., 10 mi. S of Kamuli, 1160 m, 27 May 1953, *Wood 760* (K); Western, Mubende, Singo, 1–2 mi. SE of Kikandwa, 1200 m, 16 Mar. 1969, *Lye 2354* (K). ZAÏRE. **Kivu:** Beni, Mutsora, Parc National Albert, 1200 m, 26 Mar. 1955, *De Witte 12092* (K); Yangambi, 21 May 1938, *Louis 9479* (K); Rutshuru, plaine route de Djombo, 28 Mar. 1937, *Ghesquiere 3918* (K, SRGH).

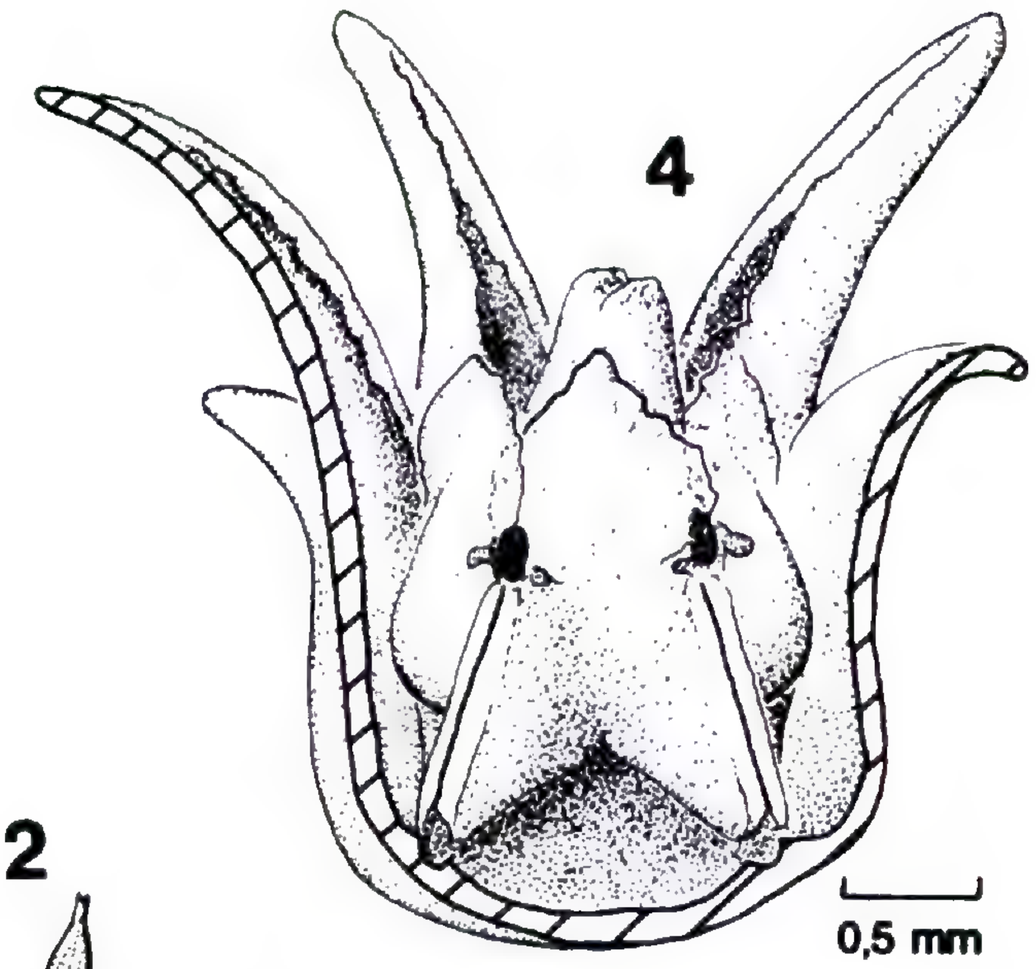
Comments. *Cynanchum polyanthum* K. Schum. can be treated as a new species, because the name was published without citing the earlier *Vincetoxicum* (*Cynoctonum*) *polyanthum* K. Schum. as bassionym; the latter represents a later homonym to *Vincetoxicum polyanthum* Kuntze.

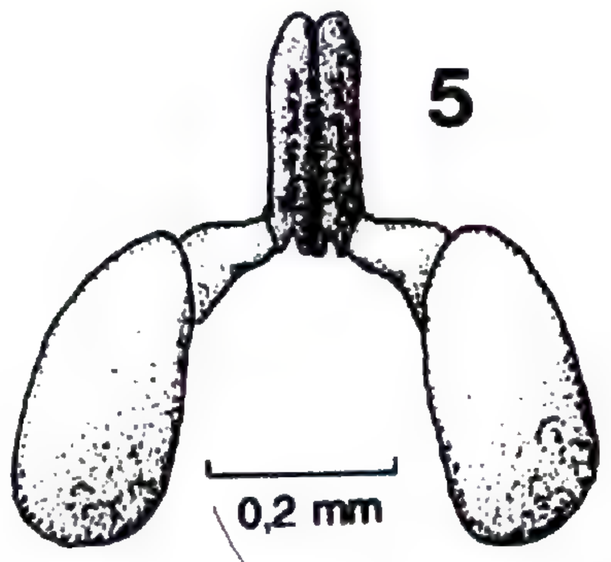
The affinities of *C. polyanthum* remain obscure. Its closest relatives are probably *C. heteromorphum* and *C. falcatum* from Ethiopia.

24. Cynanchum praecox Schlechter ex S. Moore, J. Bot. 40: 256. 1902. TYPE: Zimbabwe. Harare, valley of Mazoe River, Sep. 1898, *Rand 512* (holotype, BM). Figure 25.

Cynanchum pygmaeum Schltr., Bot. Jahrb. Syst. 51: 140. 1913. TYPE: Cameroon. Bamenda, ca. 3 mi. from Kumbo along Oku rd., 1850 m, 15 Feb. 1958, *Hepper 2011* (neotype, designated here, K); syntypes cited in the protologue: *Ledermann 2226, 2230* (both probably destroyed in B, no isotypes found).

Plants erect, nontwining, 3–10 cm high, unbranched, with rhizomes 1.5–3 mm diam. *Shoots* herbaceous, densely covered with erect trichomes, 0.35–0.4 mm long, along a single line; internodes 3 mm diam. "*Stipules*" absent. *Leaves* absent at the time of flowering, sessile, leaf blades herbaceous, 40–60 mm long, 2–8 mm wide, linear to elliptic to ovate, basally decurrent, without colleters, apically acute, marginally straight and thickened, adaxially and abaxially glabrous. *Inflorescences* supported by inflorescence bracts different from the vegetative leaves, bostrychoid, 5–15-flowered, all flowers open at a time; rachis 1–2 mm long; inflorescence bracts ca. 0.9 mm long, 0.5 mm wide, ovate, with apiculate apex, ciliate; peduncles 4–6(–8) mm long, sparsely covered with erect trichomes 0.35–0.4 mm





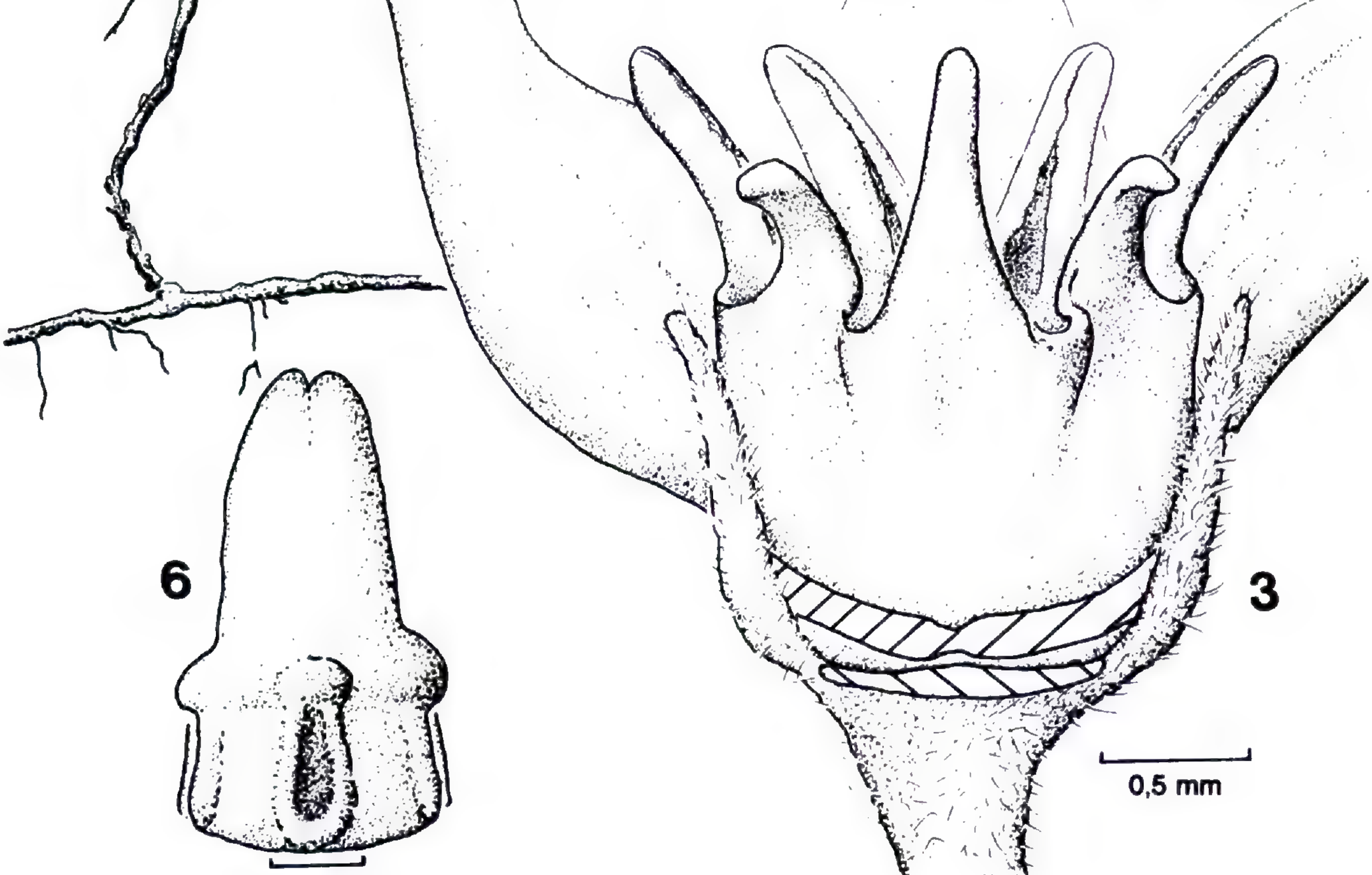


Figure 25. *Cynanchum praecox* Schltr. ex Moore.—1. Habit (*Hepper 2011*). 2–6: *Drummond 4893*.—2. Inflorescence with young fruits.—3. Flower, corolla partially removed.—4. Gynostegium and corona, partially removed.—5. Pollinarium.—6. Stylar head. Drawn by Jim Conrad.

long, along a single line. *Flowers* with a musky scent; floral bracts 0.5–0.7 mm long, 0.2–0.3 mm wide at the base, triangular, with trichomes; pedicels 5–15 mm long, densely covered with erect trichomes 0.4–0.45 mm long. *Buds* 6–6.5 mm long, 3–3.5 mm diam., elongated-conical, with imbricate aestivation, dextrorse. *Calyx* basally fused, ciliate; lobes 1.5–2.5 mm long, 0.7–0.8 mm wide, triangular, apically acute. *Corolla* rotate, fused for about ⅕ of total length; 5.5–6.5 mm long, abaxially and adaxially yellowish brown; lobes 0.5–1 mm wide, incurved, oblong, apically acute, with revolute margins. *Corona* white, 2–4 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci fused for more than half of total corona length, Cs and Ci differentiated, Ci as long as Cs, urceolate to campanulate. *Cs* not adnate to the filaments, appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, ovate, apically erect, with laterally slightly involute margins. *Lobes of Ci* laminar, oblong, reflexed, with straight margins. *Gynostegium* 1–1.1 mm high, 0.8–0.9 mm diam., sessile. *Stamens* without free filaments; anthers broader than high, trapezoidal, abaxially planar; anther wings 0.45–0.5 mm long, parallel to each other, extending beyond the anther proper, stamens forming a basal arch, adjacent anther wings parallel, centrifugal. Connective appendages 0.4–0.45 mm long, 0.35–0.4 mm wide, ovate, equaling the stamen in width, erect, with emarginate margins. *Pollinarium*: corpusculum 0.2–0.25 mm long, ovoid, margins of the corpuscular cleft sinuate; caudicles 0.05–0.06 mm long, flattened, straight, horizontal, rectangular; pollinia laterally attached to the caudicles, 0.22–0.25 mm long, 0.12–0.13 mm wide, ovoid, round in cross section. *Stylar head* 1–1.2 mm diam., 1.5–1.8 mm high; upper part 1–1.2 mm high, capitate. Mature *fruits, seeds,* and *chromosome number* unknown.

Distribution and habitat. Africa: Cameroon, Malawi, Nigeria, Sierra Leone, Tanzania (T1, T4, T7), Zaïre, Zambia, Zimbabwe; 1500–2500 m; burnt savanna and grasslands. Rare, but very widespread. Probably undercollected because of its small size. Figure 23.

Flowering time. August to February.

Selected specimens examined. CAMEROON. Bamenda, Kumbo, ca. 3 mi. along Oku rd., 1850 m, 15 Feb. 1958, *Hepper 2011* (K). MALAWI. North, Mzimba, Vipya Plateau, 3 mi. in Vipya link road, 1900 m, 25 Sep. 1972, *Pawek 5814* (K, MAL, MO); Rumpi, Nyika Plateau, Chelinda bridge, 1500 m, 10 Sep. 1976, *Pawek 11793* (K, MO). NIGERIA. Ca. 5 km N of Lana, 15 Feb. 1941, *Milne-Redhead 5030* (K). SIERRA LEONE. Kabala, Loma Mountains, 8 Jan. 1966, *Adam 22989* (MO). TANZANIA. Lake. Bukoba, Bugene, 1660 m, 21 July 1947, *Ford 190* (K). Southern Highlands. Rungwe, Mbogo Mtn., 2250 m, 7 Nov. 1966, *Gillett 17641* (EA). Western. Buha, Kibondo, 1500 m, 7 Aug. 1950, *Bullock 3096* (K); Ufipa, Mbisi, Ufipa Plateau, 2500 m, 6 Oct. 1950, *Bullock 3419* (K). ZAÏRE. Garamba-Bagbele (parc nat.), Uele, 3 Feb. 1950, *De Saeger 106 g* (K). ZAMBIA. Abercorn, Kawimbe, ca. 3 mi. from on Kara rd., 1500 m, 29 Aug. 1956, *Richards 6027* (K). ZIMBABWE. Harare, Makabusi woodlands, upper Chiravra R. near entrance gate, 10 Sep. 1981, *Best 1647* (MO).

Comments. Both syntypes of *Cynanchum pygmaeum* have been destroyed in B, and duplicate specimens, or any specimens annotated "*C. pygmaeum*" in Schlechter's handwriting, were not found. Therefore, the name has to be neotypified.

Bulllock (1953) presented a detailed account on *C. praecox* and established the synonym of *C. praecox* and *C. pygmaeum.*

The closest relative of *C. praecox* clearly is *C. orangeanum,* which is found south of the area of *C. praecox.* The affinities of these two sister species, however, remain obscure.

25. Cynanchum rubricoronae Liede, sp. nov. TYPE: Somalia. Nugaal: Aska, near Las Anod, 28 Oct. 1944, *Glover & Gilliland 199* (holotype, K). Figure 26.

Plantae habitu foliisque *C. crassiantherae.* Differt structura coronae gynostegialis roseae succulentis, partibus staminalibus oblongis erectisque, partibus interstaminalibus liguliformibus, reflexisque.

Plants erect, nontwining, 20–40 cm high, sparsely basicaulously branched. *Shoots* herbaceous, warty (*Kuchar 16793*), glabrous; internodes 20–40 cm long, 1–1.5 mm diam. "*Stipules*" ovate, 10–12 mm long, 6–7 mm wide. *Leaves* with petioles 15–20 mm long; leaf blades fleshy, 25–40 mm long, 15–24 mm wide, triangular, basally lobate to auriculate, lobes 7–10 mm long, without colleters, apically acuminate, acumen 0.5–1 mm long, marginally thickened, crenulate, adaxially and abaxially glabrous. *Inflorescences* 10–20-flowered, all flowers open at a time, bostrychoid to sciadioidal; peduncles 0–2.5 mm long, sparsely covered with flexuous trichomes 0.4–0.5 mm long. *Flowers* with floral bracts 1–1.2 mm long, 0.2–0.3 mm wide at the base, linear, with trichomes; pedicels 5–7 mm long, glabrous. *Buds* 3–3.5 mm long, 1.5–1.7 mm diam., conical, with imbricate aestivation. *Calyx* basally fused; abaxial surface glabrous; lobes 1.6–1.7 mm long, 0.4–0.5 mm wide, triangular, apically acute. *Corolla* rotate, basally fused; 3–3.5 mm long, abaxially and adaxially cream; lobes 0.7–0.8 mm wide, incurved, ovate, apically acute to apically obtuse. *Corona* basally purplish red, fading to white

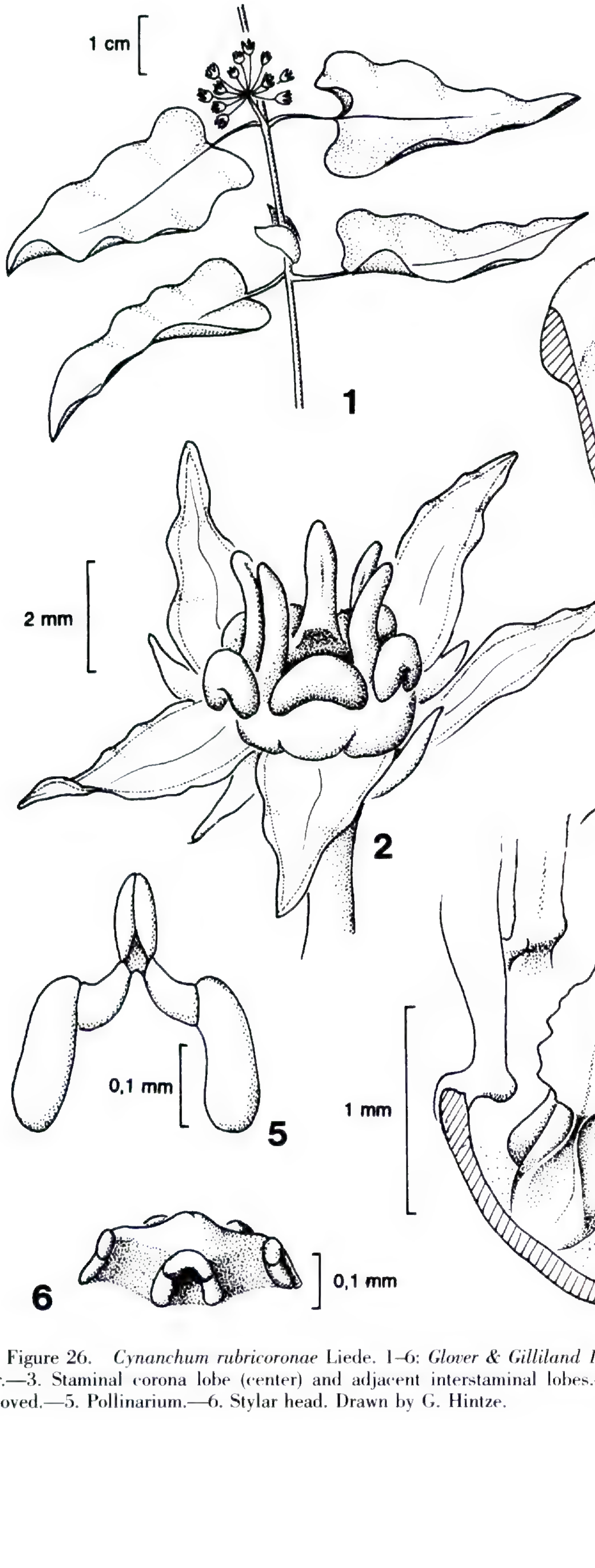


Figure 26. *Cynanchum rubricoronae* Liede. 1–6: *Glover & Gilliland 190.*—1. Shoot with inflorescence.—2. Flower.—3. Staminal corona lobe (center) and adjacent interstaminal lobes.—4. Gynostegium and corona, partially removed.—5. Pollinarium.—6. Stylar head. Drawn by G. Hintze.

toward the apex, 1.8–2 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for a little more than ½ of total corona length, Cs and Ci differentiated, Ci shorter than Cs, thicker than Cs. *Cs* not adnate to the filaments, apically appressed to the back of the stamens, without adaxial appendages; lobes of Cs laminar, oblong, apically erect, with straight margins. *Lobes of Ci* solid, massive, reflexed, flatly lingulate. *Gynostegium* 0.8–1 mm high, 0.8–1 mm diam., sessile. *Stamens* without filament, anthers broader than high, trapezoidal, abaxially planar; anther wings 0.3–0.4 mm long, convergent, very vaguely differentiated, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther, basally forming a distinct "mouth" with the basal lateral margin of the anther. Connective appendages 0.3–0.4 mm long, 0.4–0.5 mm wide, ovate, equaling the stamen in width, slightly inflexed, with emarginate margins. *Pollinarium*: corpusculum 0.14–0.16 mm long, ovoid; caudicles 0.12–0.13 mm long, flattened, concavely recurved, trapezoid; pollinia laterally attached to the caudicles, 0.26–0.28 mm long, 0.1–0.12 mm wide, oblongoid, ovate in cross section. *Stylar head* 0.3–0.4 mm diam., 0.17–0.2 mm high; upper part ca. 0.05 mm high, umbonate. *Follicles* one per flower, pendulous, ca. 70 mm long, 7 mm diam., obclavate, apically strongly beaked, wingless, light brown, with dark brown mottling, smooth, glabrous. *Seeds* and *chromosome number* unknown.

Distribution and habitat. Africa: Somalia; ca. 300 m; sandplains, hills with shrubland. From the scanty documentation in herbaria, the species appears to be very rare and is probably endangered. Figure 12.

Flowering time. May, October.

Additional specimens examined. SOMALIA. Hiiran, Bulo Burte, 23 km from Yasoomman along rd. to Maxaas, then SE 3½ km along cutline, then NE 2 km along cutline, 285 m, 1 May 1985, *Kuchar 16793* (K); Noogaal, 124 km NW of Eil, on the road to Gardo, 5 Jan. 1973, *Bally & Melville 15561* (K, MO).

Comments. *Cynanchum rubricoronae* is a very distinctive plant with quite attractive flowers. Its closest relative is probably the Somalian *C. crassiantherae*, with which it shares vegetative characters. However, its corona morphology is very distinct and is unique in the genus.

The two paratypes cited are rather poor (*Bally & Melville 15561* is completely without flowers) and are assigned to *C. rubricoronae* only tentatively.

26. Cynanchum rungweense Bullock, Kew Bull. 10: 622. 1956. TYPE: Tanzania. Mbeya: Mbeya, below Mporoto, Inkuyu, 17 Mar. 1932, *St. Clair-Thompson 846* (holotype, K). Figure 27.

Plants ascending, twining, 5–6 m high, richly and irregularly branched. *Subterranean organs* woody rootstocks. *Shoots* perennial, herbaceous, sparsely covered with appressed trichomes 0.4–0.5 mm long, along a single line, glabrescent; internodes 3–6.5 cm long, 0.8–1 mm diam. "*Stipules*" widely ovate, 4–6 mm long, 6–8 mm wide, acuminate. *Leaves* with petioles 15–30 mm long; leaf blades herbaceous, 40–50 mm long, 14–20 mm wide, ovate, basally cordate to lobate, lobes 4–6 mm long, with 2 colleters in the adaxial sinus, apically acute, adaxially dark green, sparsely covered with appressed trichomes 0.4–0.5 mm long, restricted to veins and margins, abaxially much paler green, papillose, glabrous. *Inflorescences* bostrychoid to sciadioidal, 12–16-flowered, 6–9 flowers open at a time; rachis to 2 mm long; peduncles 10–30 mm long, glabrous to densely covered with erect trichomes 0.2–0.3 mm long, along a single line. *Flowers* with floral bracts 1.3–1.4 mm long, 0.4–0.5 mm wide at the base, elongate-triangular, apically glandular, with trichomes; pedicels 11–15 mm long, densely covered with flexuous trichomes 0.3–0.35 mm long. *Buds* 5–7 mm long, 3–4 mm diam., conical, with imbricate aestivation. *Calyx* basally fused, abaxial surface glabrous; lobes 1.6–1.8 mm long, 1.2–1.4 mm wide, ovate, apically obtuse to acute. *Corolla* rotate, basally fused; 6–7 mm long, abaxially green, adaxially greenish brown; lobes 2.5–3 mm wide, horizontal, oblong, apically obtuse. *Corona* urceolate, white, 4.5–5 mm high, exceeding the gynostegium, partly obscuring it; C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, Cs and Ci differentiated, Ci slightly longer than Cs. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, triangular, apically erect. *Lobes of Ci* laminar, triangular, erect. *Gynostegium* 1.6–1.7 mm high, 1.8–2 mm diam., atop a stipe, 0.55–0.66 mm long. Anthers broader than high, pentagonal, abaxially planar; anther wings 0.8–1 mm long, convergent, extending along the whole length of the anther; adjacent anther wings parallel, basally centrifugal. Connective appendages 0.7–0.75 mm long, 0.5–0.55 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.3–0.35 mm long, more than twice as long as broad, obovoid; caudicles 0.45–0.5 mm long, apically cylindrical, then flattened, s-shaped, convex-concave;

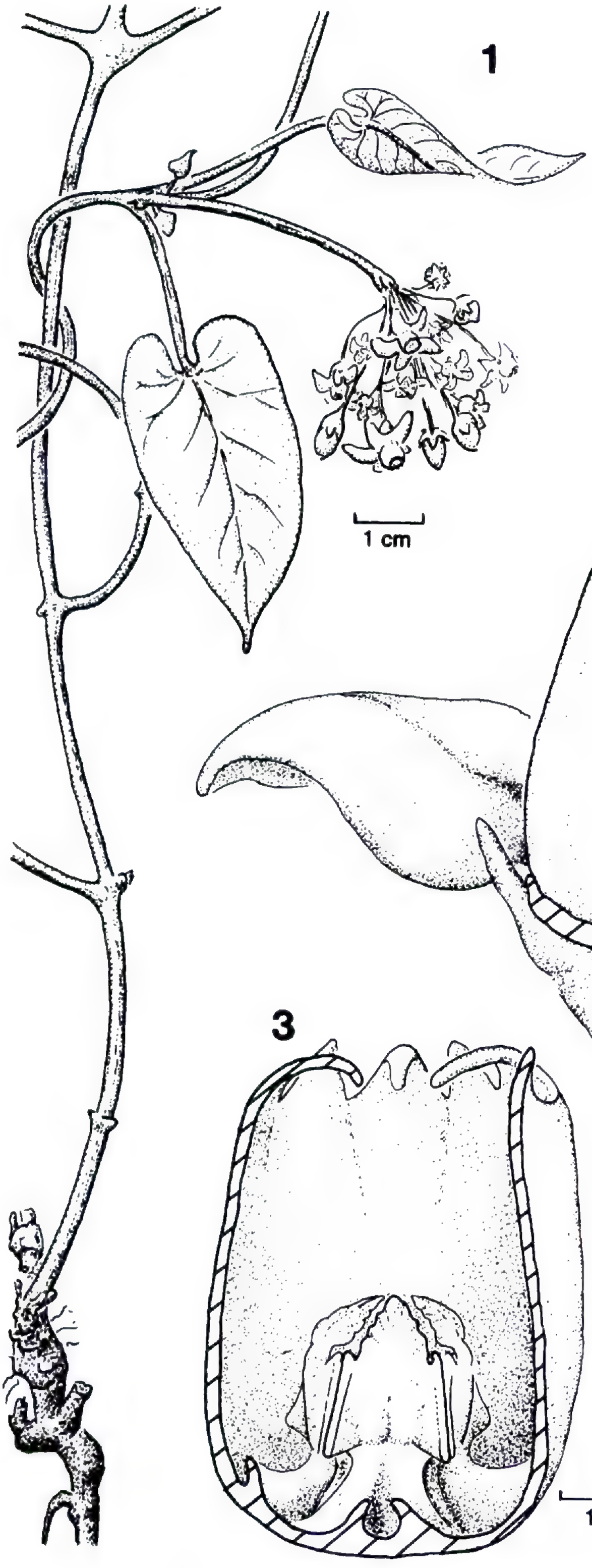


Figure 27. *Cynanchum rungweense* Bullock.—1. Habit (*Goyder 3269*) and inflorescence (*Leedal 4015*). 2–5: *Dowsett-Lemaire 236*.—2. Flower, corolla partially removed.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head. Drawn by Jim Conrad.

pollinia apically attached to the caudicles, 0.58–0.6 mm long, 0.24–0.26 mm wide, ovate in cross section, pyriform. *Stylar head* 1.3–1.5 mm diam., 0.3–0.4 mm high; upper part 0.05–0.1 mm high, shorter than the lower part, umbonate. *Fruits, seeds,* and *chromosome number* unknown.

Distribution and habitat. Africa: Malawi, Tanzania (T7), Zambia; 1700–2600 m; forests and forest margins. Fairly localized and infrequent, but probably not threatened. Figure 8.

Flowering time. October to March, May.

Vernacular name. Ilago (Safwa).

Selected specimens examined. MALAWI. North, Rumpi, Station Kyimbila, Nyassa Hochland, 2000 m, 19 Dec. 1911, *Stolz 1034* (B, K, M). TANZANIA. **Iringa:** Mufindi, Luisenga Stream, forest path by stream, 1830 m, 3 Jan. 1987, *Lovett 1303* (K, MO). **Mbeya:** Mbeya range, World's End view, Ipinda, 2660 m, 6 Feb. 1976, *Cribb, Grey-Wilson & Mwasumbi 10576* (K). **Ruvuma:** near Uwemba village, 18 km S of Njombe, 12 km from Njombe–Songea rd., ca. 2200 m, 27 Nov. 1986, *Brummitt, Goldblatt, Lovett & Mwasumbi 18209* (K). ZAMBIA. Eastern (FZ), Chama, Nyika Plateau, S of Zambian Rest House, 21 May 1989, *Goyder, Pope & Radcliffe-Smith 3269* (K).

Comments. *Cynanchum rungweense* is one of the more attractive, relatively large-flowered species of the genus. It belongs to the *C. altiscandens* group with a very highly fused corona and a stipitate gynostegium. Its closest relative is probably *C. altiscandens.*

Schlechter was obviously aware of this species, as it is found under the name *Cynanchum stolzii* Schltr. in several herbaria. However, the name was never published, so *C. rungweense* Bullock is the valid name for the taxon.

Cribb and Leedal (1982: 105) reported *C. rungweense* from the mountains of southern Tanzania.

27. Cynanchum schistoglossum Schlechter, J. Bot. 33: 271. Sep. 1895. TYPE: South Africa. Natal. Stanger, Phoenix, Apr. 1895, *Schlechter 7090* (neotype, B; isoneotypes, AMD, BM); syntypes cited in the protologue: *Schlechter 7106, Taylor 1895* (both probably destroyed in B, no isotypes found).

Cynanchum brevidens N. E. Br., Bull. Misc. Inform., Kew 1895: 257. Oct. 1895. TYPE: Congo, Sep. 1863, *Burton s.n.* (holotype, BM).

Cynanchum brevidens N. E. Br. var. *zambesiaca* N. E. Br., Bull. Misc. Inform., Kew 1895: 257. Oct. 1895. TYPE: Mozambique. Expedition Island, July 1838, *Kirk s.n.* (holotype, K).

Cynanchum vagum N. E. Br., Bull. Misc. Inform., Kew 1895: 257. Oct. 1895. TYPE: Zaïre. Stanley Pool, 26 Aug. 1888, *Hens 77* (holotype, K). *Cynanchum minutiflorum* K. Schum., Bull. Soc. Roy. Bot. Belg. 37: 123 (1898), nom. illeg., because Schumann cited *Hens 77,* the type of *Cynanchum vagum* N. E. Br., as type.

Cynanchum dewevrei De Wild. & T. Durand, Ann. Mus. Congo, Ser. 1, Bot. Ser. 2, 1(2): 42. 1900. TYPE: Zaïre. Mwanana Toumbwé, 27 July 1890, *Dewèvre 904* (lectotype, designated here, BR).

Plants twining, to 3 m high, richly branched; rhizomatous; rhizomes 1–2 mm diam. *Subterranean organs* woody rootstocks. *Shoots* perennial, 1–1.5 mm diam., herbaceous, sparsely glabrescent with erect trichomes 0.3–0.4 mm long. "*Stipules*" ovate, 3–7 mm long, 2–5 mm wide. *Leaves* with petioles 10–25 mm long, leaf blades herbaceous, 35–60 mm long, 15–35 mm wide, ovate-lanceolate to ovate, basally cuneate or cordate to lobate with 4 colleters in the adaxial sinus, apically acute to acuminate, adaxially isolatedly covered with erect trichomes 0.3–0.4 mm long, evenly distributed over the whole surface, abaxially sparsely covered with erect trichomes 0.3–0.4 mm long restricted to veins and margins. *Inflorescences* bostrychoid, 5–20-flowered, 5–10 flowers open at a time; rachis 1–2 mm long; peduncles 5–12 mm long, densely covered with erect trichomes 0.3–0.4 mm long. *Flowers* musky scented; floral bracts 1 mm long, 0.5 mm wide at the base, triangular, with trichomes; pedicels 3–8 mm long, densely covered with appressed trichomes 0.3–0.4 mm long. *Buds* 1–1.5 mm long, 1–1.5 mm diam., globose; aestivation imbricate. *Calyx* entirely free, abaxially with trichomes; lobes 0.8–1.2 mm long, 0.4–0.6 mm wide, triangular, apically acute. *Corolla* cyathiform, 1.2–3.5 mm long, abaxially with a few isolated trichomes, adaxially glabrous, whitish to yellowish green; lobes 0.8–1 mm wide, incurved, lanceolate, apically acute to acuminate. *Corona* white, cyathiform, 1.2–1.7 mm high, equaling the gynostegium; C(is) consisting of Cs and Ci fused for ½–¾ of total corona length, Cs and Ci differentiated in shape; Ci shorter and thinner than Cs, laterally connate to Cs. *Cs* adnate to the filaments for not more than ⅓ of total corona length, appressed to the back of the stamens, without adaxial appendages; lobes of Cs flat, equally bifid or trifid with the two lateral lobes much smaller than the medium one, inflexed with straight margins. *Lobes of Ci* flat, triangular, erect with straight margins. *Gynostegium* 0.75–1 mm high, 0.8–1.1 mm diam., sessile. *Stamens* with free filaments 0.1–0.2 mm long, anthers broader than high, trapezoidal, abaxially planar; anther wings 0.375–0.45 mm long, paralleling the anther, extending along the whole length of the anther, adjacent anther wings parallel, in the same plane as the anther; outer guide rail smooth; connective appendages 0.3–0.4

mm long, 0.4–0.5 mm wide, widely ovate, narrower than the stamen, strongly inflexed; margins emarginate, slightly bifid. *Pollinarium*: corpusculum 0.14–0.15 mm long; margins of the corpuscular cleft parallel; caudicles 0.09–0.1 mm long, cylindrical, straight, horizontal; pollinia laterally attached to the caudicles, 0.2–0.25 mm long, 0.09–0.1 mm wide, ovoid, ovate in cross section. *Stylar head* 0.7–0.9 mm diam., 0.3–0.35 mm high; upper part 0.1–0.15 mm high, depressed-conical. *Follicles* 50–55 mm long, 5–6 mm wide, fusiform, round in cross section, apically obtuse, medium brown, smooth, glabrous. *Seeds* 4.5–5 mm long, 3.5–4 mm wide, ovate, light brown, seta and aseta side almost smooth, with 0.4–0.5 mm wide wing with distally dentate margin; coma 20–25 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Angola, Botswana, Burundi, Kenya (K4), Malawi, Mozambique, Namibia, Rwanda, South Africa (Natal, Transvaal), Tanzania (T2, T3, T4, T6), Uganda (U2, U4), Zaïre, Zambia, Zimbabwe; 0–1800 m; on clayey loam; forest margins, thickets, grasslands; often near water, also roadsides and disturbed areas. Figure 18.

Flowering time. All year, with peak between April and October.

Selected specimens examined. ANGOLA. Golungo Alto, Punto de Felix Simoes, June 1856, *Welwitsch 4241* (K); Huilla, near Lopollo, Oct. 1895, *Welwitsch 4251* (K). BOTSWANA. Mochudi, Jan.–Apr. 1914, *Rogers 6617* (BOL, PRE); Ngamiland, E bank of Okavanga river, near boundary with SWA, ca. 1020 m, 27 Apr. 1975, *Müller & Biegel 2282* (K, MO, PRE, SRGH); Northern, Bushman Pits, Botlethe River at Loromoja, 22 Apr. 1975, *Ngoni 408* (K, MO, PRE, SRGH); Nokaneng, Nokaneng, 20 mi. from the abandoned village of Kanozo, 1 June 1967, *Lambrecht 220* (K, SRGH). BURUNDI. Bubanza, plaine de la Rusizi, km 14, 850 m, 18 May 1974, *Reekmans 3456* (K, MO); Bujumbura, Aérodrome, 800 m, 28 Apr. 1967, *Lewalle 1852* (K). KENYA. **Central:** North Nyeri, Nyeri, 19 Dec. 1921, *Fries & Fries 139* (K). MALAWI. Between Kondowe and Kawanga, 2000–2300 m, June 1890, *Whyte s.n.* (K); Mamitete River below bridge on Lilongwe–Ft. Jameson Rd., 1150 m, 5 Feb. 1959, *Robson 1464* (K). MOZAMBIQUE. Momba, Managra, 13 July 1949, *Faulkner 459* (K); Barada, 21 July 1950, *Chase 2230* (K, SRGH). NAMIBIA. Andara, bei Dikundu, im Omuramba (19.2 km S Andara), 15 June 1971, *Giess 11436* (PRE). RWANDA. Biumba, colline Karukwanzi, région du Mutara, près de la river Kakitumba, 21 Mar. 1958, *Troupin 6762* (MO). SOUTH AFRICA. **Natal:** Durban, Merebank, S.W., 19 Feb. 1967, *Baijnath 132* (PRE); Pietermaritzburg, Inanda, July 1880, *Wood 611* (BM); Port Shepstone, Isipingo Rail (Platts Estate), ca. 13 m, 7 Apr. 1966, *Ward 5548* (PRE); Stanger, near Umhlanga river, 24 Apr. 1895, *Wood 5664* (BOL, MO, PRE); Umzinto, Hazlewood, 6 Apr. 1967, *Baijnath 287* (PRE). **Transvaal:** Acornhoek, 1½ mi. E of Skukuza, Kruger National Park, 300 m, 5 Apr. 1949, *Codd 5491* (PRE). TANZANIA. **Arusha:** Sakila, rd. to Sakila swamp, 1500 m, 14 Sep. 1971, *Richards 27219* (K, MO). **Morogoro:** Uluguru Gebirge, ca. 1200 m, 30 June 1933, *Schlieben 4044* (K, MO). **Rukwa:** Sakalilo (nr), 1000 m, 25 May 1951, *Bullock 3896* (K). **Ruvuma:** Ilonga, 530 m, 20 June 1967, *Robertson 733* (K). **Tabora:** near Kisanga, ca. 700 m, 19 Aug. 1970, *Thulin & Mhoro 765* (K). **Tanga:** Korogwe, Kisarake, near Mnyusi Railway station, 30 Apr. 1971, *Semsei 4239* (K). UGANDA. Ankole, Mitoma, 1500 m, Mar. 1939, *Purseglove 600* (K); Kigezi, Kanungu, 1830 m, June 1939, *Purseglove 821* (K); Mengo, Mulange, 1430 m, Sep. 1919, *Dümmer 4306* (BM, K); Toro, near Sempayo, Oct. 1924, *Liebenberg 947* (K). ZAÏRE. Dolo (Congo), June 1899, *Schlechter 12485* (K, L). ZAMBIA. Chipata, Musandile, Nsefu, Luangwe valley, 12 Apr. 1968, *Phiri 158* (K, SRGH); Lundazi, 4 mi. S of Lundazi Boma, 27 Apr. 1952, *White 2479* (K, MO); near Chilanga, Mt. Makulu Research Station, 24 Mar. 1962, *Angus 3078* (K). ZIMBABWE. Kasungula, Oct. 1855, *Gairdner 546* (K); Victoria Falls, S. Bank of Zambesi, 1000 m, May 1915, *Rogers 13125* (BOL).

Comments. Neither of the two syntypes of *Cynanchum schistoglossum* could be traced and both have probably been destroyed in B. The specimen selected as neotype was collected and identified by Schlechter and can thus be considered to conform to his concept of the species.

Schumann (1895) published *C. minutiflorum* as nomen nudum and only typified it three years later on *Hens 77*, the type specimen of *C. vagum* N. E. Br.

Of the two well-preserved syntypes of the description of *C. dewevrei* (*Dewèvre 904* and *976a*, both in BR), the one with the more precise collection data has been chosen as lectotype.

Cynanchum schistoglossum is perhaps the most variable species on the African mainland. Corona dentation and degree of fusion differ considerably among the populations. The species can be recognized by the very small flowers (smallest-flowered species on the African mainland) and the distinct fusion of the staminal corona parts with the filaments, which is only found in *C. gerrardii* and *C. lenewtonii*, with which it also shares the characteristic shape of the anthers and anther wings.

28. Cynanchum somaliense (N. E. Brown) N. E. Brown in Dyer, Fl. Trop. Afr. 4(1): 398. 1903. *Schizostephanus somaliensis* N. E. Br. in Bull. Misc. Inform., Kew 1895: 250. 1895. *Cynanchum trifurcatum* Schltr., Bull. Herb. Boissier 4: 448. 1896, nom. nov. TYPE: Somalia. Boobi, *James & Thrupp s.n.* (holotype, K). Figure 28.

Cynanchum dentatum K. Schum., Annuario Reale Ist. Bot. Roma 7: 39. 1898. TYPE: Somalia. Inter Sassaber et Cabaden iter duorum dierum a Mil-Mil et Ogaden distans locis aridis silvaticis, Jan., *Riva 844* (holotype, FT).

Figure 28. *Cynanchum somaliense* (N. E. Br.) N. E. Br. 1, 2: *Gilbert & Thulin 1510*; 3–7: *Mesfin & Vollesen 4238*; 8: *Friis et al. 3221*.—1. Habit.—2. Node with inflorescence.—3. Flower, corolla partially removed.—4. Gynostegium and corona, partially removed.—5. Corona lobe, adaxially.—6. Pollinarium.—7. Stylar head.—8. Fruit. Drawn by Jim Conrad.

Plants erect or ascending, twining, 1–4 m high, sparsely basicaulously branched, with rhizomes. *Shoots* herbaceous, sparsely covered with flexuous trichomes 0.3–0.4 mm long; internodes 4–11 cm long, 0.8–2 mm diam. "*Stipules*" ovate, apiculate, 10–12 mm long, 7–10 mm wide. *Leaves* with petioles 15–45 mm long, leaf blades herbaceous, 30–85 mm long, 20–60 mm wide, ovate, basally cordate to lobate, lobes 3–5 mm long, with 5–7 colleters in the adaxial sinus, apically acute to acuminate, adaxially and abaxially isolatedly covered with appressed trichomes 0.3–0.4 mm long, concentrated on veins and margins. *Inflorescences* bostrychoid, 10–15-flowered, 6–8 flowers open at a time; rachis 1 mm long; peduncles 10–30 mm long, densely covered with flexuous trichomes 0.2–0.3 mm long, along a single line. *Flowers* aromatically scented (fide *Gillett 13340*); floral bracts 1.4–1.8 mm long, 0.3 mm wide at the base, linear, with trichomes; pedicels 4–7 mm long, densely covered with flexuous trichomes 0.2–0.3 mm long. *Buds* 1.6–1.8 mm long, 1.4–1.5 mm diam., cylindrical (apically widened), with imbricate aestivation. *Calyx* basally fused; abaxial surface glabrous; lobes 2–2.2 mm long, 0.6–1.1 mm wide, ovate to oblong, apically acute. *Corolla* rotate; basally fused; 3.5–4 mm long, abaxially yellowish purple, adaxially yellow; lobes 1–1.2 mm wide, patent, cucullate, apically obtuse. *Corona* white, changing to purplish red with age, 3–3.5 mm high, equaling the gynostegium; C(is) consisting of Cs and Ci only basally fused, only Cs differentiated. *Cs* not adnate to the filaments, without adaxial appendages; lobes of Cs laminar, trifid (central lobe internally with two strong folds), apically erect. *Gynostegium* 1–1.2 mm high, 2–2.2 mm diam., atop a stipe 2.2–2.3 mm long. *Stamens* without free filaments, anthers broader than high, deltoid, abaxially convex; anther wings 0.4–0.45 mm long, divergent, not extending along the whole length of the anther; the anther forming a "pseudostipe" 0.6–0.7 mm high; adjacent anther wings parallel, basally widened, in the same plane as the anther. Connective appendages ca. 0.25 mm long, 0.7–0.8 mm wide, ovate, equaling the stamen in width, strongly inflexed. *Pollinarium*: corpusculum ca. 0.3 mm long, more than twice as long as broad, elliptic; caudicles ca. 0.8 mm long, cylindrical, straight, declinate; pollinia apically attached to the caudicles, 0.75–0.8 mm long, 0.25–0.3 mm wide, ovoid, ovate in cross section. *Stylar head* white, 1.1–1.2 mm diam., 0.3–0.35 mm high; upper part 0–0.05 mm high, flat to umbonate. *Follicles* one per flower, 50–60 mm long, 8–10 mm diam., obclavate, apically obtuse, medium brown, sparsely covered with 3–5-mm-long protuberances, with sparse indumentum. *Seeds* approximately 60–80 per follicle, marginally winged (only immature seeds known). *Chromosome number* unknown.

Distribution and habitat. Africa: Ethiopia (Bale, Haverge, Sidamo, Welo), Kenya (K1, K4), Somalia (Hiiraan, Sanaag, Woqooyi Galbeed/Todgheer), Sudan, Tanzania (T1), Uganda (U1, U4); 350–1700 m, *Acacia–Commiphora* bushland, open shrub, and grasslands. Widespread and fairly common. Figure 10.

Flowering time. March to November.

Vernacular names. Goriss (Boran), gasur riyoli (Ogaden), yapo (Uganda).

Uses. Helps women in childbirth, also for abdominal pains (*Dyson-Hudson 224, 225, 226*).

Selected specimens examined ETHIOPIA. **Bale:** between Gaad and Harrana, ca. 860 m, 26 Sep. 1964, *Burger 3524* (EA); Haverge, Scillave, 630 m, 11 Apr. 1956, *Simmons 141* (K). **Sidamo:** Borana, 46 mi. SE of Neghelle, on Filtu-Dolo Road, 1450 m, 4 Apr. 1974, *Ash 2425* (K, MO). **Welo:** below Back on Assab rd., 700 m, 19 Sep. 1962, *Mooney 9662* (WAG). KENYA. **Central:** Meru, 13 km N of Isiolo on road to Marsabit, 1050 m, 11 Feb. 1978, *Gilbert, Gachathi & Gatheri 5314* (K, MO); North Nyeri, Nan, Ngare Ndare Farm, 1500 m, 19 Apr. 1981, *Gilbert 6093* (K). **Northern Frontier:** Mandera, 2 km N of El Wak, 30 Apr. 1978, *Gilbert & Thulin 1265* (K). SOMALIA. Hiiraan, Bulo Burti, ca. 25 km along the rd. to Buqda Caqable, then 5 km SW along cutline, 180 m, 17 May 1986, *Kuchar 17017* (K, MO); Sanaag, 32 km S of Erigavo, 1340 m, 26 Nov. 1980, *Hemming & Watson 3279* (K); Woqooyi Galbeed/Todgheer, Boundary Pillar 93, 1100 m, 10 Apr. 1932, *Gillett 4173* (K). SUDAN. Imatong Mts., just S of Ngarama, along rd. to Molongori, near northernmost point of cont. mountain chain, 700 m, 13 Mar. 1986, *Friis & Vollesen 1189* (K). TANZANIA. **Mwanza:** Igalukiro, Narso, Mwanza, 1200 m, 18 July 1953, *Tanner 1597* (K). UGANDA. Karamoya, near Emonayaben, Nabilatuk, 1200 m, 26 June 1957, *Dyson-Hudson 226* (K); Mengo, Buvuma, Namunyoro, *Maitland 1190* (K).

Comments. Schlechter (1896) suggested *Cynanchum trifurcatum* as a nomen novum for *Cynanchum somaliense* (N. E. Br.) N. E. Br., stating that there was another species known by the name of *Cynanchum somaliense*. However, he neither indicated an author of this species, nor is any such species known to me as validly published. Therefore, there is no need to rename *Cynanchum somaliense* (N. E. Br.) N. E. Br.

Cynanchum somaliense has long been regarded as the closest relative of *Schizostephanus alatus*. However, while this judgment was derived from the long stipe and the seemingly similar pollinarium structure, *Schizostephanus* has recently been identified as a member of a different subtribe (Liede, 1993). While long stipes have been developed sev-

eral times independently, the unique fine structure of the pollinarium of *Schizostephanus* has been illustrated in Liede (1993). Liede and Nicholas (1992) have deduced that the corona in *Pentarrhinum* can be interpreted morphologically as a development from the type found in *P. somaliense.* The close relationship of *C. somaliense* and *Pentarrhinum* is further supported by the wingless follicles with soft spines. *Schizostephanus,* in contrast, possesses smooth follicles with conspicuous wings.

29. Cynanchum umtalense Liede, sp. nov. TYPE: Zimbabwe. Melsetter: Chirinda Forest Margin, ca. 1200 m, Jan. 1962, *Goldsmith 1/62* (holotype, K; isotypes, B, BR, FI, SRGH). Figure 29.

Volubilis. Corollae lobis introrsum pilis singularibus ornatis; partibus staminalibus coronae gynostegialis ligulatis; capite stylorum longe elongato.

Plants ascending, twining, 5–6 m high, richly and irregularly branched. *Shoots* perennial, herbaceous, densely covered with flexuous trichomes 0.7–0.8 mm long; internodes 7–10 cm long, 0.5–1 mm diam. "*Stipules*" absent. *Leaves* with petioles 15–20 mm long, leaf blades herbaceous, 35–70 mm long, 15–45 mm wide, ovate, basally cordate to obtuse with 2–3 colleters in the adaxial sinus, apically acuminate (acumen 2–3 mm long), adaxially and abaxially sparsely covered with appressed trichomes 0.6–0.8 mm long evenly distributed over the whole surface. *Inflorescences* sciadioidal, 7–11-flowered, 2–5 flowers open at a time; peduncles 7–15 mm long, densely covered with flexuous trichomes 0.5–0.6 mm long. *Flowers* with floral bracts 1.6–1.8 mm long, 0.4–0.5 mm wide at the base, triangular, with trichomes; pedicels 8–10 mm long, densely covered with flexuous trichomes 0.4–0.5 mm long. *Buds* 5–6 mm long, 2–2.5 mm diam., conical, basally with imbricate, apically with contorted aestivation. *Calyx* basally fused; abaxial surface with trichomes; lobes 1.4–1.6 mm long, 0.7–0.8 mm wide, ovate, apically acute. *Corolla* rotate, basally fused; 6–7 mm long, abaxially with trichomes, adaxially cream, rose to purple along the main nerves; adaxially with verrucose trichomes 0.1–0.12 mm long, evenly distributed over the whole surface; lobes 1.8–2 mm wide, apically twisted, patent to recurved, linear to triangular, apically obtuse to acute. *Corona* white, 2.3–2.5 mm high, equaling the gynostegium (except for stylar head appendage); C(is) consisting of Cs and Ci fused for more than ¾ of total corona length, Cs and Ci differentiated, Ci shorter than Cs. *Cs* not adnate to the filaments, with adaxial appendages; lobes of Cs lobes laminar, triangular, apically erect; appendages of Cs slightly longer than Cs, laminar, triangular, erect. *Lobes of Ci* laminar, rectangular, producing a pronounced convex fold along the upper third of corona length, erect, with straight, emarginate margins. *Gynostegium* 1.6–1.8 mm high (without stylar head appendage), 1.6–1.8 mm diam., sessile. *Stamens* without free filaments, anthers about as high as broad, rectangular, abaxially planar; anther wings 0.7–0.8 mm long, parallel to each other, extending along the whole length of the anther; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.5–0.6 mm long, 0.7–0.8 mm wide, ovate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.2–0.22 mm long, rhomboid; caudicles 0.09–0.1 mm long, flattened, straight, horizontal, triangular; pollinia subapically attached to the caudicles, 0.3–0.35 mm long, 0.12 mm wide, clavate, ovate in cross section. *Stylar head* white, 0.5–0.6 mm diam., 2.5–2.6 mm high; upper part 2.3–2.4 mm high, obinfundibuliform. *Follicles* one per flower, 45 mm long, 6–8 mm diam., obclavate, keeled, apically shortly beaked, medium brown, with dense indumentum. *Seeds* 6.5–7 mm long, 3.5–4 mm wide, ovate, medium brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.3-mm-wide wing with entire margin; coma 18–20 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Malawi (North, Central), Zimbabwe (Melsetter, Umtali); 1200–2000 m; forest margins. A fairly infrequent species with a rather limited distribution, but probably not immediately threatened because it grows inside forest reserves. Figure 2.

Flowering time. January, April to July.

Specimens examined. MALAWI. Central. Dedza, Dedza Mountain, 1750 m, 5 Apr. 1978, *Pawek 14228* (BR, K, MAL, MO, WAG); lower eastern slopes of Domwe Hill, above Trinidad's Place, 1 Apr. 1961, *Chapman 1212* (K). North. Nkhata Bay, 3 km S of Chikangawa, 1950 m, 10 July 1978, *Phillips 3515* (K, MAL, MO, SRGH, WAG). ZIMBABWE. Umtali, Vumba Mts., 28 Apr. 1957, *Chase 6465* (B, FI, K, SHRG), 4 June 1957, *Chase 6541* (K), 2 Apr. 1958, *Chase 6866* (K), 12 May 1957, *Pole-Evans 5210* (K); Hawkdale, Vumba, 29 Jan. 1957, *Chase 6562* (K).

Comments. Cynanchum umtalense is a very distinctive species, but clearly identifiable as a member of the group with verrucose trichomes on the corolla lobes and ligules; probably closest to *Cynanchum abyssinicum.*

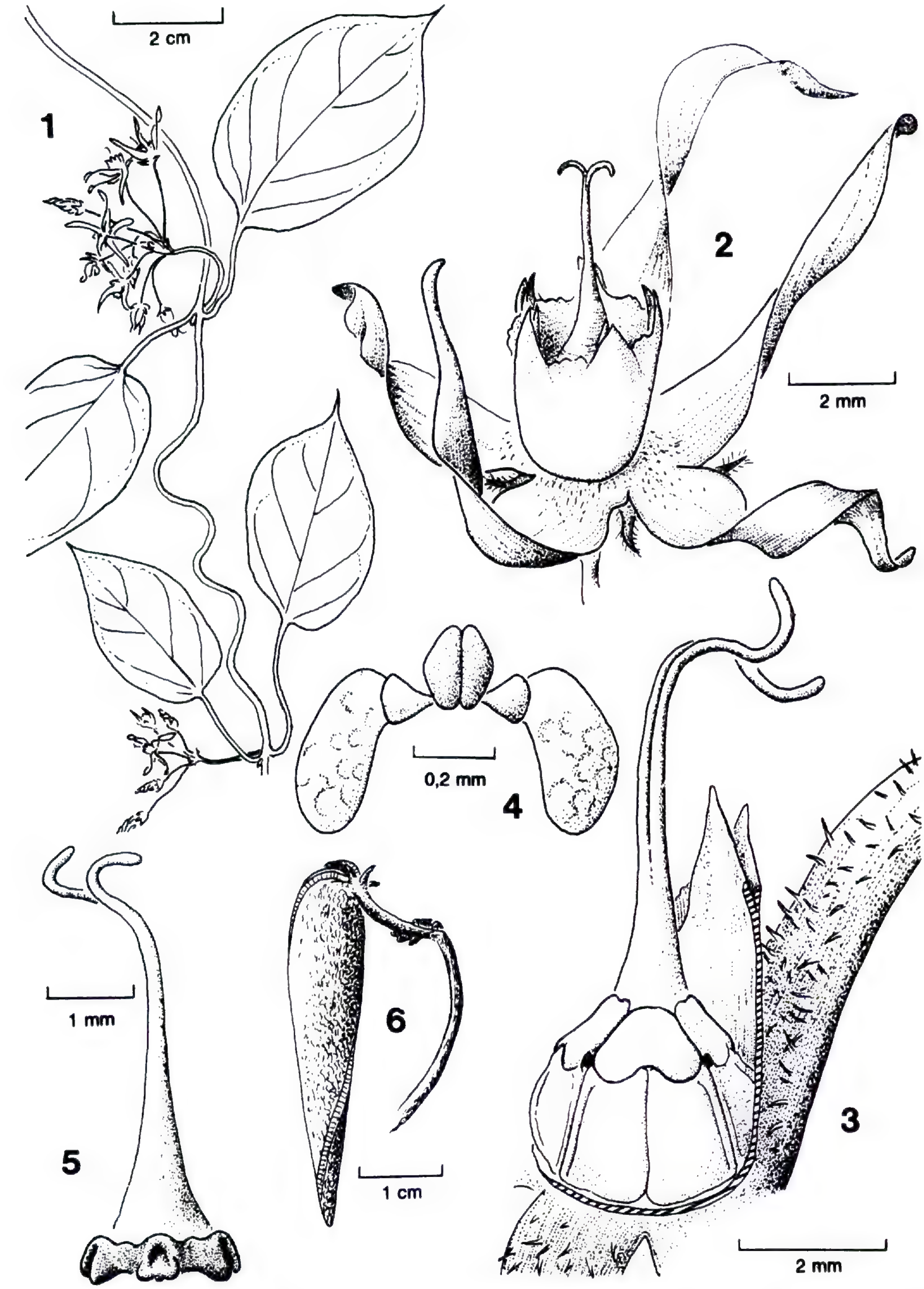


Figure 29. *Cynanchum umtalense* Liede. 1–5: *Chase 6866*; 6: *Chase 2562*.—1. Habit with inflorescences.—2. Flower.—3. Gynostegium and corona, partially removed.—4. Pollinarium.—5. Stylar head.—6. Fruit. Drawn by Jim Conrad.

30. Cynanchum virens (E. Meyer) D. Dietrich, Syn. Pl. 2: 905. 1840. *Cynoctonum virens* E. Mey., Comm. Pl. Afr. Austr. 216. 1838. *Cynanchum virens* (E. Mey.) Steud., Nomencl. Bot. (ed. 2) 1: 462. 1841, nom. superfl. *Vincetoxicum virens* (E. Mey.) Kuntze, Revis. Gen. Pl. 2: 424. 1891. *Endotropis meyeri* Decne. in Candolle, Prodr. 8: 546. 1844, nom. superfl. TYPE: Namibia. Garip, 19 Dec. 1832, *Drège 3439* (lectotype, designated by Liede (1993), P).

Not *Cynanchum virens* (E. Mey.) D. Dietr., Syn. Pl. 2: 906. 1840, based on *Schizoglossum virens* E. Mey., Comm. Pl. Afr. Austr. 219. 1838. TYPE: South Africa. Natal: inter Omsamcaba et Port Natal, *Drège s.n.*, as cited by Schlechter, Bot. Jahrb. Syst. 20, Beih. 51: 7. 1895 (see comments).

Plants twining, 0.5–1 m high, sparsely branched; subterranean organs rhizomatous; rhizome 10–15 mm diam. *Shoots* perennial, 50–100 cm long, 1 mm diam., herbaceous, glabrous, or isolatedly to sparsely covered with appressed trichomes 0.25–0.3 mm long, basally woody with yellowish bark. "*Stipules*" ovate, 3–5 mm long, 2–5 mm wide. *Leaves* with petioles 10–25 mm long; leaf blades herbaceous, 30–50 mm long, 15–30 mm wide, lanceolate, basally cordate with 4 colleters in the adaxial sinus, apically acute, abaxially and adaxially glabrous to isolatedly indumented with appressed trichomes 0.25–0.3 mm long, evenly distributed over the whole surface. *Inflorescence* bostrychoid to sciadioidal, 7–15-flowered, 3–8 flowers open at a time; rachis to 0.5 mm long; peduncles 2–10 mm long, glabrous isolatedly covered with appressed trichomes 0.25–0.3 mm long. *Flowers* with floral bracts 0.8–1 mm long, 0.2–0.3 mm wide at the base, linear to triangular, with trichomes; pedicels 5–7 mm long, glabrous to isolatedly covered with erect trichomes 0.25–0.3 mm long. *Buds* 4–4.5 mm long, 2.5–3 mm diam., elongated-conical; aestivation imbricate. *Calyx* basally fused, abaxially glabrous or with trichomes; lobes 1–1.5 mm long, 0.5–0.7 mm wide, triangular, apically acute. *Corolla* rotate, fused at the base, 6–8 mm long, abaxially glabrous, greenish white, adaxially with verrucose trichomes, whitish green; lobes 1–1.5 mm wide, spreading, ovate, apically acuminate, twisted. *Corona* white, cyathiform, 5–5.5 mm high, exceeding the gynostegium but not obscuring it; C(is) consisting of Cs and Ci fused for ca. ⅓ of corona length, both Cs and Ci differentiated in shape, Ci shorter and thinner than Cs, dorsally connate to Cs. *Cs* adaxially with adaxial appendages; lobes of Cs flat, long-apiculate, inflexed, with straight margins; adaxial appendages shorter than Cs, erect, liguliform. *Lobes of Ci* flat, ovate, erect, with straight, denticulate margins. *Gynostegium* sessile, 1.4–1.6 mm high, 1–1.2 mm diam. *Stamens* without free filaments; anthers about as high as broad, trapezoidal, abaxially planar, anther wings 0.55–0.6 mm long, parallel to each other, extending beyond the anther proper forming a basal arch; adjacent anther wings parallel, in the same plane as the anther. Connective appendages 0.6–0.65 mm long, 0.5–0.55 mm wide, deltate, narrower than the stamen, slightly inflexed. *Pollinarium*: corpusculum 0.2–0.22 mm long; margins of the corpuscular cleft sinuate; caudicles 0.14–0.16 mm long, flattened, straight, horizontal, triangular; pollinia laterally attached to the caudicles, 0.32–0.35 mm long, 0.14–0.16 mm wide, ovoid, round in cross section. *Stylar head* 0.6–0.75 mm diam., 0.8–1 mm high, upper part 0.57–0.6 mm high, conical. *Follicles* 50–60 mm long, 15–20 mm wide, obclavate, obtusely deltate in cross section, apically shortly to strongly beaked, keeled, light to dark brown, longitudinally grooved, glabrous. *Seeds* 5–5.5 mm long, 3–4 mm wide, ovate, medium to dark brown, seta and aseta side sculptured with longitudinal ridges, marginally with 0.4–0.6-mm-wide wing with entire margin; coma 20–25 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: Lesotho, Namibia, South Africa (Cape Province, Transvaal, Orange Free State); 1200–2000 m, flats and gentle slopes; sandy to loamy soil; riverine vegetation; partial shade.

Comments. Dietrich (1840: 905, 906) published two combinations as *Cynanchum virens* (E. Mey.) D. Dietr., one based on *Cynoctonum virens* E. Mey., the other one on *Schizoglossum virens* E. Mey. Schlechter (1895) is the only author using the latter, because all other authors regard *Schizoglossum*, a member of the subtribe Asclepiadinae, as well distinct from *Cynanchum*.

Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

31. Cynanchum zeyheri Schlechter, Bot. Jahrb. Syst. 20, Beibl. 51: 3. 1895. TYPE: *Ecklon & Zeyer 78* (lectotype, designated by Liede (1993), SAM).

Plants decumbent, 15–20 cm high, richly branched; subterranean organs consisting only of fibrous roots. *Shoots* perennial, 15–20 cm long, 1–1.5 mm diam., herbaceous, glabrous, or isolatedly to sparsely covered with appressed trichomes 0.15–

0.2 m long, basally woody with yellowish bark. "*Stipules*" 2–3 mm long, 3–4 mm wide. *Leaves* with petioles 5–10 mm long; leaf blades herbaceous, 10–15 mm long, 5–10 mm wide, ovate, basally rounded, without colleters, apically obtuse, or acute and apiculate, adaxially and abaxially glabrous. *Inflorescence* sciadioidal, 2–5-flowered, all flowers open at a time; peduncles 0.5–5 mm long, glabrous to isolatedly covered with appressed trichomes 0.15–0.2 mm long. *Flowers* sweetly scented; floral bracts 0.7–1 mm long, 0.2–0.5 mm wide at the base, triangular, papillose; pedicels 5–10 mm long, glabrous. *Buds* 3.5–4 mm long, 1–1.5 mm diam., elongate-conical; aestivation imbricate, apically contorted. *Calyx* basally fused, abaxially glabrous; lobes 1–1.5 mm long, 0.5–0.8 mm wide, ovate, apically acute and apiculate. *Corolla* rotate, fused at the base, 3–4 mm long, abaxially glabrous, brown, adaxially minutely papillose brown; lobes ca. 1 mm wide, spreading, oblong, apically obtuse, mostly twisted, with revolute margins. *Corona* white, tubular to campanulate, 1.5–2 mm high, shorter than the gynostegium; C(is) consisting of Cs and Ci fused for about ¾ of total length, only Cs differentiated in shape. *Cs* without adaxial appendages; lobes of Cs flat, ovate, erect, with straight margins. *Gynostegium* 0.7–0.8 mm high, 0.8–1 mm diam., atop a stipe, 0.7–1 mm long. *Stamens* without free filaments; anthers trapezoid, abaxially rounded; anther wings 0.25–0.3 mm long, clearly differentiated, paralleling the anther, parallel to each other, extending along the whole length of the anther margin; connective appendages 0.55–0.6 mm long, 0.4–0.45 mm wide, ovate, narrower than the stamen, erect. *Pollinarium*: corpusculum 0.13–0.14 mm long; caudicles 0.07–0.08 mm long, flattened, straight, horizontal to declinate, triangular; pollinia 0.3–0.35 mm long, 0.12–0.13 mm wide, clavate, elliptical in cross section. *Stylar head* 1–1.1 mm diam., 0.5–0.55 mm high; upper part 0.47–0.5 mm high, conical. *Follicles* 35–45 mm long, 12–15 mm wide, club-shaped, sharply deltate in cross section, apically shortly beaked, wingless, light brown to medium brown, longitudinally grooved, glabrous. *Seeds* 5–6 mm long, 4–5 mm wide, pyriform, medium brown, seta and aseta side tuberculate (but less pronouncedly so on the seta side); marginally with indistinct wing 0.2–0.3 mm wide, with entire margin; coma 20–25 mm long. *Chromosome number* unknown.

Distribution and habitat. Africa: South Africa [Cape Province, disjunction Cape Peninsula (Lionshead)–Bredasdorp]; 0–1000 m; flats to moderate slopes; shales and limestone; fynbos, renosterveld, strandveld.

Comments. Further details, illustration, distribution map, and citation of specimens are provided in Liede (1993).

Excluded Species

Cynanchum aphyllum (Thunb.) Schltr. = *Sarcostemma viminale* (L.) R. Br. (Liede, 1991)

Cynanchum arboreum Forssk. = *Leptadenia arborea* (Forssk.) Schweinf.

Cynanchum atropurpureum (E. Mey.) D. Dietr. = *Schizoglossum atropurpureum* E. Mey.

Cynanchum argel Delile = *Solenostemma argel* (Delile) Hayne

Cynanchum bidens (E. Mey.) D. Dietr. = *Schizoglossum bidens* E. Mey.

Cynanchum boveanum Decne. = *Glossonema boveanum* (Decne.) Decne.

Cynanchum chirindense S. Moore = *Tylophora* sp.

Cynanchum cordifolium (E. Mey.) D. Dietr. = *Schizoglossum* sp.

Cynanchum crispum Thunb. = *Gomphocarpus crispus* (P. J. Bergius) W. T. Aiton

Cynanchum defoliascens K. Schum. = *Blyttia fruticulosum* (Decne.) D. V. Field & J. R. I. Wood

Cynanchum filiforme L. f. = *Schizoglossum* sp. fide Schlechter (1895)

Cynanchum fruticulosum Decne. = *Blyttia fruticulosum* (Decne.) D. V. Field & J. R. I. Wood

Cynanchum gossweileri S. Moore = *Schizostephanus gossweileri* (S. Moore) Liede

Cynanchum hamatum (E. Mey.) D. Dietr. = *Schizoglossum hamatum* E. Mey.

Cynanchum heterophyllum Delile = *Leptadenia heterophylla* (Delile) Decne.

Cynanchum lancifolium Schumach. & Thonn. = *Leptadenia lancifolium* (Schumach.) Decne.

Cynanchum latifolium Schumach. & Thonn. = *Leptadenia lancifolium* Decne.

Cynanchum linifolium (Balf. f.) Bullock = *Vincetoxicum linifolium* Balf. f.

Cynanchum mauritianum Bojer ex Decne. = *Tylophora laevigata* Decne.

Cynanchum microstegium K. Schum. = *Blyttia fruticulosum* (Decne.) D. V. Field & J. R. I. Wood

Cynanchum molle (E. Mey.) D. Dietr. = *Anisotoma cordifolia* Fenzl

Cynanchum oleaefolium Nectoux = *Solenostemma argel* (Delile) Hayne

Cynanchum omissum Bullock = *Fockea angustifolia* K. Schum.

Cynanchum ovatum Thunb. = *Leptadenia reticulata* (Retz.) Wight

Cynanchum pendulum Poir. = *Leptadenia* sp.
Cynanchum radians (Forssk.) Lam. = *Odontanthera radians* (Forssk.) D. V. Field
Cynanchum reticulatum Retz. = *Leptadenia reticulata* (Retz.) Wight
Cynanchum roseum Chiov. = *Tylophora heterophylla* A. Rich.
Cynanchum scabrum Schumach. & Thonn. = Marsdenieae sp.
Cynanchum senegalense Sieber ex Decne. = *Gymnema subvolubile* (Schumach.) Decne.
Cynanchum subvolubile Schumach. & Thonn. = *Gymnema subvolubile* (Schumach.) Decne.
Cynanchum tetrapterum (Turcz.) R. A. Dyer = *S. viminale* (L.) R. Br.
Cynanchum validum N. E. Br. = *Schizostephanus alatus* Hochst. ex K. Schum.
Cynanchum verticillare Lam. = *Schizoglossum* sp. fide Schlechter (1895)
Cynanchum viminale L. = *Sarcostemma viminale* (L.) R. Br.

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PHYLOGENY AND SPECIATION IN *LAPEIROUSIA* SUBGENUS *LAPEIROUSIA* (IRIDACEAE: IXIOIDEAE)[1]

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ABSTRACT

A cladistic analysis of southern African subgenus *Lapeirousia*, one of two subgenera of the exclusively African genus *Lapeirousia*, yielded four equally parsimonious trees, one of which is identical with the strict consensus tree. Characters used in the analysis included growth form, corm morphology, a range of floral characters, and capsule and seed features, not before known to vary significantly in this genus. The analysis suggested some surprising evolutionary changes. Notable among these is an apparent reversal of perianth tube length from extremely long to short, a shift corresponding to a change from pollination by long-tongued flies and sphinx moths to pollination by bees and noctuid moths. Another unusual change is a shift in floral organization from zygomorphy to actinomorphy correlated with an acaulescent growth form. The reconstructed phylogeny is used here to assess character evolution and patterns of speciation by comparison of species in terminal clades in the cladograms. The resulting comparisons suggest that speciation in the subgenus is either allopatric or the result of microgeographic differentiation and ecological diversification stimulated by edaphic diversity. Despite the variety of floral forms and pollination syndromes in the subgenus there is no evidence of sympatric or pollinator-driven speciation. Prepollination reproductive isolation appears to be achieved by shifts in pollination syndromes between sphinx moths, two guilds of long-tongued flies, and bees. The remarkable floral divergence that has resulted appears to be a consequence of selection for repeated entry into preexisting pollination guilds. The most important of these pollination guilds are two long-tongued fly guilds in which either *Prosoeca* (Nemestrinidae) or *Moegistorhynchus* (Nemestrinidae) and *Philoliche* (Tabanidae) are pollinators. These two guilds are also likely to have been important in promoting speciation in other genera and families in the southern African flora.

The flora of southern Africa is rich and unusually diverse for an area falling predominantly in temperate latitudes (Goldblatt, 1978). Some 20,400 species of native vascular plants are currently recognized in the region (Arnold & de Wet, 1993), of which about 80% are endemic (Goldblatt, 1978). The major factors proposed to account for the species richness are climatic, edaphic, and topographic diversity and a history of paleoclimatic change in the late Tertiary (Goldblatt, 1978). Although these factors may permit the existence of large numbers of species, they do not indicate the modes of speciation that have led to this diversity. One method of inferring modes of speciation is by comparing biological attributes of closely related, and by extension evolutionarily recent, sister species. Differences in biology between such species give an indication of the factors that led to speciation. Cladistic analysis is a critical method for identifying sister species. A detailed phylogenetic hypothesis such as a cladogram makes it possible to trace backwards in time the series of evolutionary events that gave rise to the modern taxonomic distribution of ecological features even in the absence of fossil information (Armbruster, 1993). This in turn makes it possible to develop specific hypotheses on the evolution of species diversity (Manning & Linder, 1992).

The tropical and southern African genus *Lapeirousia* Pourret comprises some 40 species segregated in two subgenera each with two sections (Goldblatt & Manning, 1990, 1992, 1994). Subgenus *Lapeirousia* (21 species) is centered in coastal and near interior southwestern Africa. This is a semiarid region of low to moderate winter rainfall and extreme summer drought. Two species are widespread in the southwestern and southern parts of Western Cape Province, South Africa, and a further two occur in tropical Africa (Goldblatt, 1990b). Subgenus *Paniculata* (19 species) comprises the largely tropical African section *Paniculata* (14 species), with one species in the southwestern part of southern Africa (Goldblatt & Manning, 1992), and section *Fastigiata* (5 species), which is restricted

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to the southwestern part of Western Cape Province. Field studies of subgenus *Lapeirousia* conducted over the past three years have provided a wealth of information about the ecology and biology of its 21 species, and this has enabled us to develop a detailed understanding of the group. This has provided an objective measure of relationships among the species that in turn lays the foundation for analyses of changes in pollinator preferences and patterns of radiation and speciation. We use the reconstructed phylogeny of subgenus *Lapeirousia* and the inferred modes of speciation to address questions of how its species coexist and how they might have evolved. We expect these hypotheses to have more general application for plant speciation in southern Africa.

Materials and Methods

CHARACTERS AND TAXA

Subgenus *Lapeirousia* is believed to be monophyletic and the sister clade to subgenus *Paniculata* (Goldblatt & Manning, 1990), the outgroup for the cladistic analysis. The subgenus is regarded here as comprising 21 species (Goldblatt, 1972, 1990b; Goldblatt & Manning, 1994). Both subspecies of *L. pyramidalis* (subsp. *regalis* and subsp. *pyramidalis*) are included in the analysis because they differ in some important characters, and we were unwilling to assign arbitrary plesiomorphic states for the species. Morphological and anatomical characters (Table 1) were assembled from the above systematic treatments, and supplemented by new data presented here.

For the cladistic analysis 24 characters were ultimately selected (Table 1; Appendix). These included all macromorphological aspects of the plants, as well as capsule and seed surface morphology, not known until now for most species. Seed characters of all species of *Lapeirousia* were investigated for this study. Seeds vary both in primary and secondary sculpturing, and provided valuable characters for the cladistic analysis (Appendix: characters 6, 7, and 8). Chromosome cytology (Goldblatt & Takei, 1993) was not included in the cladistic analysis, but was used to assess the trees that were generated. Basic chromosome number for *Lapeirousia* is probably $x = 10$, but the base number for subgenus *Lapeirousia* appears to be $x = 9$ (Goldblatt, 1990a; Goldblatt & Takei, 1993). Multistate characters of an additive nature, e.g., corm tunic bases lobed, lightly denticulate, coarsely dentate, were treated as ordered (characters 2, 6, 7, and 14).

ECOPHYLOGENY

Data on pollination and habitat were recorded for each species in subgenus *Lapeirousia* and mapped onto the cladogram (Fig. 4). The ecological characteristics of the lower nodes were determined using the operating principle of parsimony. In this way the evolutionary history of the interactions can be inferred and the sequence of evolutionary changes that have generated the current interactions can be determined (Donoghue, 1989; Brooks & McLennan, 1991; Armbruster, 1992). This methodology has been used to investigate the evolution of pollination systems in, for example, *Dalechampia* (Euphorbiaceae) (Armbruster, 1992, 1993, 1994). Data on pollination ecology are derived from Goldblatt et al. (1995).

CLADISTIC ANALYSIS

Data were analyzed using the Hennig86 package of programs for parsimony analysis (Farris, 1988), using the mh* and bb* option, followed by successive weighting. Five randomly generated taxon sequences were analyzed, with the same result being obtained. The data include considerable homoplasy (there appear to be convergent trends for some flower types in different lineages) with the result that the strict consensus tree of 1322 equally parsimonious trees resulting from unweighted computations (Fig. 1A) shows little resolution (length 74, consistency index (CI) 0.48, retention index (RI) 0.67).

Successive weighting, recommended by Farris (1969) for situations where unreliable (homoplasious) characters outnumber reliable characters, is one way to improve tree resolution. The method selectively weights those characters that are more consistent at the expense of those that are homoplasious. The method can be successful even when cladistically consistent characters are heavily outnumbered by homoplasious ones. After invoking the successive weighting option six equally parsimonious trees (CI 0.81 and RI 0.91), but only four different topologies, were obtained. The four trees differ only in minor details and correspond in most respects to our intuitive ideas about species relationships in the subgenus. The strict consensus tree obtained with successive weighting (Fig. 1B) is actually identical to one of the four final trees (Fig. 2A), and discussion is framed around this tree.

All the differences in branching patterns in the other trees are present in a second tree illustrated (Fig. 2B). The differences are alternative topologies at nodes 7 and 14. We generated one more tree using the data matrix and the same options, mh*, bb*, and successive weighting, but with *Savanno-*

Table 1. Matrix and character list for the cladistic analysis (Figs. 1–3). The outgroups are *Savannosiphon* or subgenus *Paniculata*. The features of the latter are inferred by comparison of its constituent species (no single species accords with the hypothetical ancestor). When the plesiomorphic state is uncertain for the outgroup, the character is scored as "?". Chromosome numbers were not included in the analysis, but where confidently known (Goldblatt & Takei, 1993), are indicated opposite each species in Figure 4. Character 25 is used only with the analysis with *Savannosiphon* as the outgroup (Fig. 3). Multistate characters 2, 6, 7, and 14 are treated as ordered (see Appendix 1), and 5, 8, 13, 15, and 17 are treated as unordered.

	Character number				
Taxon	111 123456	111111 789012	122222 345678	2 901234	5
Savannosiphon	0?0100	100000	201000	0010?0	0
Subgenus *Paniculata*	000?00	000000	000000	000000	1
L. pyramidalis (Lam.) Goldblatt					
subsp. *pyramidalis*	100102	011011	300101	010110	1
subsp. *regalis* Goldblatt & Manning	100102	011011	303101	010100	1
L. silenoides (Jacq.) Ker Gawl.	100101	011011	303101	110000	1
L. verecunda Goldblatt	100101	011011	302101	110000	1
L. divaricata N. E. Br.	120101	020111	111021	110011	1
L. spinosa (Goldblatt) Goldblatt	120111	001111	111021	1100?1	1
L. dolomitica Dinter	131101	001011	303011	010000	1
L. violacea Goldblatt	131101	001011	303010	110000	1
L. tenuis (Goldblatt) Goldblatt & J. Manning	131101	000011	10001?	110000	1
L. *jacquinii* N. E. Br.	110101	021011	303010	110100	1
L. fabricii (Delaroche) Ker Gawl.	121101	020111	222010	111000	1
L. barklyi Baker	111101	000111	023020	111000	1
L. simulans Goldblatt & Manning	110101	000011	302010	110000	1
L. macrospatha Baker	110111	021011	202010	011000	1
L. arenicola Schltr.	110111	021011	202000	110000	1
L. littoralis Baker	100100	101011	301000	?11010	1
L. anceps (L.f.) Ker Gawl.	100101	000011	302010	110000	1
L. odoratissima Baker	100020	101011	301000	011010	1
L. montana Klatt	100020	201011	300000	010010	1
L. plicata (Jacq.) Diels	100020	101011	200000	010000	1
L. oreogena Schltr. ex Goldblatt	100020	201011	303000	010000	1
L. exilis Goldblatt	100111	001011	200100	?10000	1

1. Corm tunics consisting of compacted fibers (0)—corm tunics woody (1)
2. Corm tunic bases lightly lobed (0)—bases minutely denticulate (1); bases coarsely and irregularly short-dentate (2); bases fairly regularly long-dentate (3)
3. Corm shape campanulate (0)—corm shape broadly conic (1)
4. Flowers actinomorphic (0)—flowers zygomorphic (1)
5. Plants with well-developed aerial stems (0)—plants forming fairly compact tufts (1); plants normally without aerial stems, i.e., acaulescent (2)
6. Seed surface cells unevenly colliculate-foveate and not in straight files (0)—cell surfaces colliculate and cells in files (1); cell surfaces tuberculate and cells in files (2)
7. Seed surface without secondary sculpturing (0)—surface with folds in a diffuse ruminate pattern (1); surface with a ± regularly reticulate pattern (2)
8. Capsules rounded in transverse section, thus without locular ridges (0)—capsules with winglike locular ridges (1); capsules with auriculate lobes decurrent on locular ridges (2)
9. Branches borne well above the ground (0)—branches mostly or only at ground level (1)
10. Lower tepals straight (0)—lower tepals geniculate (1)
11. Leaf blades plane (0)—blades plicately ribbed (1)
12. Bracts soft-textured (0)—bracts firm-textured (1)
13. Perianth tube about as long as the tepals (0)—shorter than the tepals (1); 1.5–3 times as long (2); (3–)4–6 times as long (3)
14. Perianth tube ± cylindric throughout (not abruptly widened above) (0)—tube abruptly expanded above into a flared upper part (1); tube with the upper part wide and cylindric (2)

Table 1. Continued.

15. Perianth pale blue with white and dark blue markings (0)—predominantly white (sometimes with cream or blue markings) (1); cream with red markings and reddish on the reverse (2); dark red to purple or blue to violet (3)
16. Tepals ovate to lanceolate (0)—tepals spathulate (1)
17. Surface of lower tepals plane (0)—lower tepals each with a slender cusp near the base (1); lower tepals each with a toothlike ridge at base (2)
18. Upper tepal reflexed (0)—upper tepal arched (1)
19. Outer bracts without a median fold or keel (0)—outer bracts with median fold or keel (1)
20. Inner bracts about as long as the outer (0)—two-thirds to half as long (1)
21. Flowers small (upper tepal usually less than 16 mm long) (0)—flowers large (upper tepal 18–27 mm long) (1)
22. Outer bracts acute (0)—bracts obtuse to retuse (1)
23. Flowers unscented (0)—flowers sweetly scented (1)
24. Lower and upper lateral tepals separating from the tube at the same level (0)—lower tepals joined to the upper laterals for 3–5 mm (1)
25. Corm base rounded (0)—bases flat, corm thus campanulate (1)

siphon as the outgroup, and one more character, campanulate corms, the generic synapomorphy for *Lapeirousia* (Fig. 3). Because *Savannosiphon* has been suggested to be the sister genus to *Lapeirousia* (Goldblatt, 1989) we were curious to see how the resulting trees would compare with those in which subgenus *Paniculata* is the outgroup. Trees were analyzed using CLADOS (Nixon, 1992) and the trees presented here were generated with this program.

The phylogenetic relationships were also reconstructed using PAUP 3.1.1 (Swofford, 1993) in order to utilize the bootstrap option and establish a measure of confidence in the results of the cladistic analysis (Felsenstein, 1985). A heuristic search was carried out saving minimal length trees only with the collapse zero length branches option in effect. The data were subjected to reweighting, using the maximum value of rescaled consistency indices, which is the same as successive weighting in Hennig86 (Swofford, 1993). A hundred replicates were run with the heuristic search option (limitations of time made it impractical to run more than 100 replicates), simple weighting, and with characters sampled randomly. The bootstrap values are presented on the strict consensus tree (Fig. 1B).

Results

Cladistics

On the trees illustrated (Figs. 2A, B), the character distributions as mapped show subgenus *Lapeirousia* to be supported by seven synapomorphic characters, four of which are autapomorphic and three homoplasious. The subgenus can thus reasonably be presumed to be monophyletic. The autapomorphies for the subgenus include woody corm tunics, leaf blades with plicate ridges, floral bracts firm-textured, and inner bracts about half as long as the outer (characters 1, 11, 12, 20), all universal for the subgenus. Within subgenus *Lapeirousia* the strict consensus tree indicates a primary divergence into two clades, the smaller one of which (node 2) comprises all the species with derived seeds having primary sculpturing (character 7). The clade, which includes the type of section *Sophronia* (but not all the species assigned to it by Goldblatt & Manning (1990)), also contains the two tropical African species, *L. littoralis* and *L. odoratissima*. Within this clade a group of species are apomorphic in their acaulescent habit and actinomorphic flower, a reversal which may well be closely associated with the acaulescent habit (Goldblatt, 1990b). In addition, all species of the clade at node 2 have the derived basic chromosome number, $x = 8$. Although we see no a priori reason to believe that the clade is an artifact of the analysis, in the strict consensus tree generated using *Savannosiphon* as outgroup, *L. littoralis* is one clade of a trichotomy (Fig. 3) in which the acaulescent species comprise the second clade and the remaining species of the subgenus the third. Close association of the acaulescent species and *L. littoralis* depends on how character 7 (seeds with primary sculpturing) is polarized, and this will remain uncertain until more information can be obtained about the generic relationships of *Lapeirousia*.

The second of the two primary clades (node 5) in both the trees with subgenus *Paniculata* as outgroup has either two synapomorphies (Fig. 2A), seeds with colliculate secondary sculpturing (character 6), and bracts with a median fold or keel

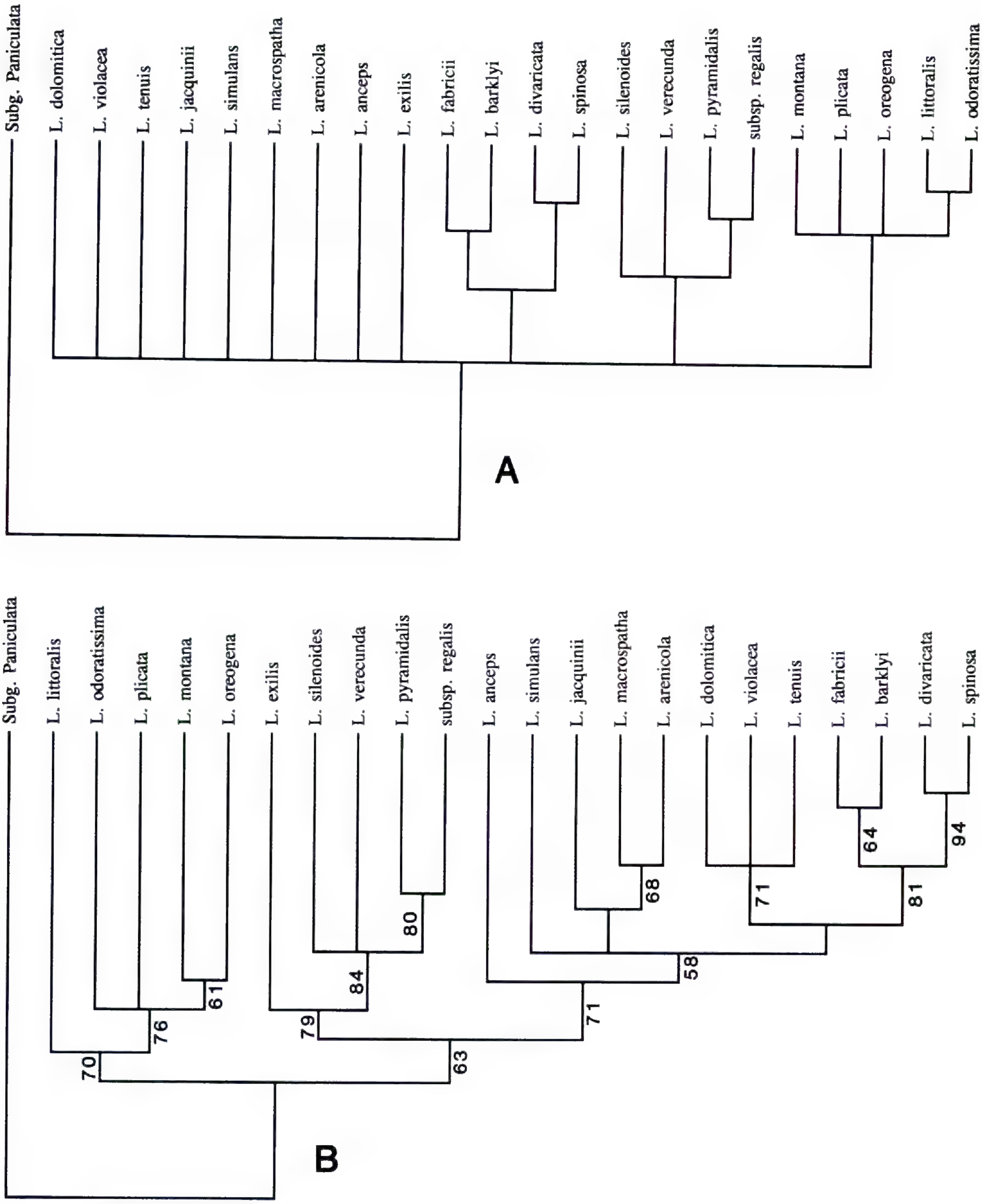


Figure 1. Strict consensus trees generated from the character matrix (Table 1).—A. Tree generated using the mh* and bb* options of Hennig86.—B. Bootstrap values drawn on the strict consensus tree generated using the mh* and bb* options of Hennig86 followed by successive weighting. The bootstrap values were calculated using PAUP and involving the maximum value of rescaled consistency index option (equivalent to successive weighting of Hennig86).

(character 19), or one synapomorphy (Fig. 2B), character 6. Within this clade there is again a primary dichotomy. Of the two resultant clades the one at node 6 is supported by one floral character, the spathulate shape of the tepals. However, the clade at node 9 has either three characters (Fig. 2A): cusps on the lower tepals (17), perianth cream with red markings (15), and the branching pattern (9), all homoplasious; or four, the last being the outer bracts folded or keeled (19) (Fig. 2B). All members

Figure 2. Cladograms generated using the mh*, bb*, and successive weighting options of Hennig86 (Farris, 1988), using the data matrix (Table 1) and subgenus *Paniculata* as outgroup.—A. Strict consensus tree of six equally parsimonious trees. The strict consensus tree is identical to one of the six trees, hence the characters are mapped on the tree.—B. One of the other five trees embodying the two differences between the strict consensus tree and the six original trees, indicated at nodes 7 and 14. Character bars mapped onto the tree are shaded as follows: black = non-homoplasious apomorphy; gray = homoplasious apomorphy; clear = reversal. Numbers above character bars refer to character numbers, those below the bars indicate the character state.

of this clade except *Lapeirousia anceps*, which is sister to the remaining species, and *L. jacquinii* are apomorphic in their corms with basal teeth or spines and chromosome numbers. In particular, *L. jacquinii* shows poor resemblance to other members of the clade in gross morphology. It shares apomorphic bracts with *L. pyramidalis*, has the plesiomorphic corm type, and may have a hybrid ori-

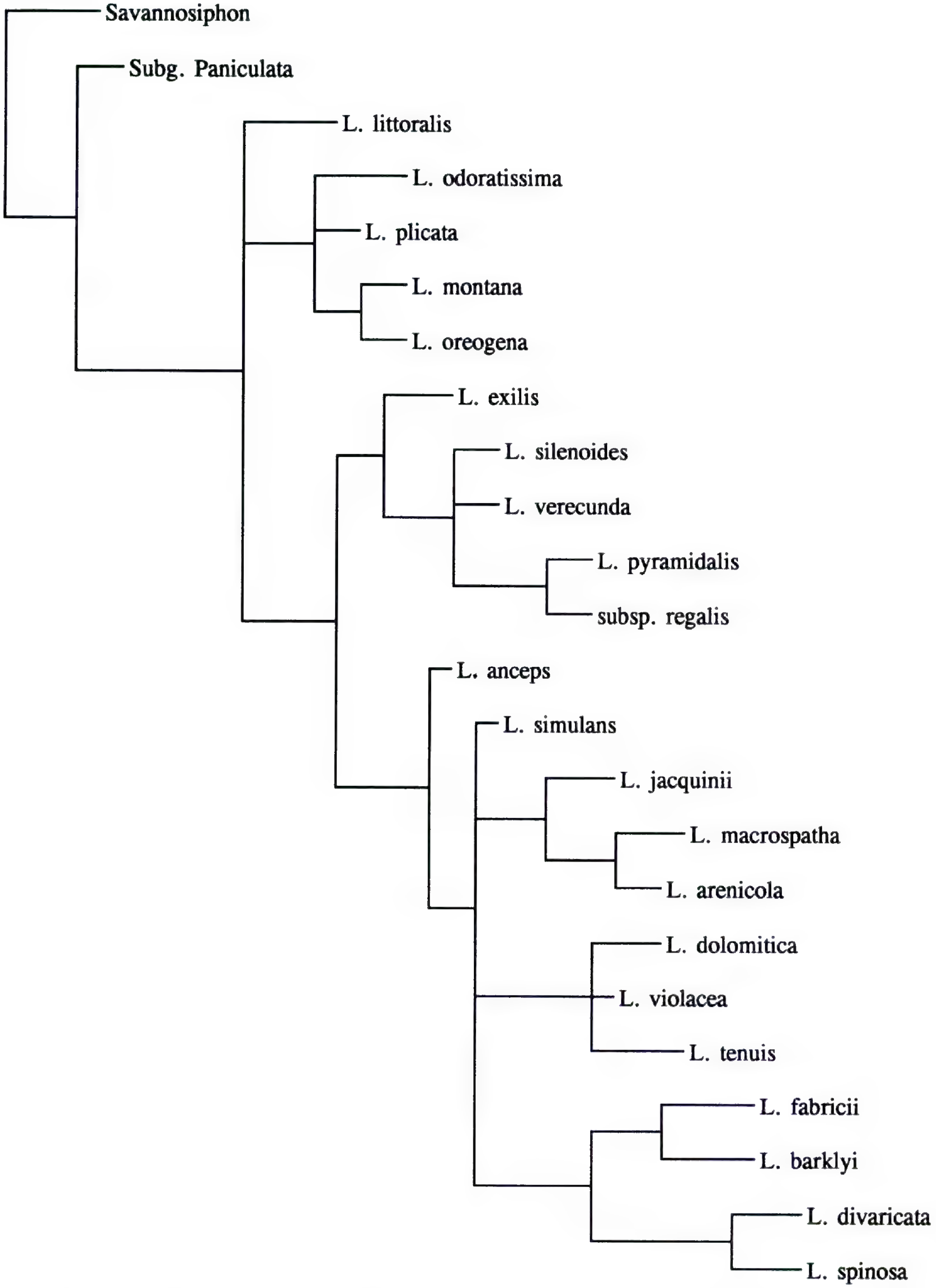


Figure 3. Strict consensus tree of seven equally parsimonious trees generated with the mh*, bb*, and successive weighting options of Hennig86 (Farris, 1988) with *Savannosiphon* as outgroup. The tree was generated using the same data matrix (Table 1) as the trees in Figures 1 and 2, plus one character, campanulate corms, apomorphic for all species of *Lapeirousia*. Scoring was changed for character 7, to reflect changed polarity.

gin. The topology of the remaining species of the clade is consistent with our intuitive ideas about relationships.

Terminal pairs in the strict consensus tree (Fig. 2A) and in the alternative equally parsimonious tree (Fig. 2B) are identical, except for *Lapeirousia silenoides-L. verecunda* and *L. dolomitica-L. violacea* (compare the topology at nodes 7 and 14 in Figs. 1 and 2). These species are terminal pairs only in Figure 2B. The number of steps to achieve the different topologies is the same (although the characters themselves differ), but we have no a priori reason to favor either alternative. The possibility that the species are terminal pairs remains a reasonable hypothesis. In the tree with *Savannosiphon* as outgroup (Fig. 3) the tree topology is the same at all the major nodes except for the position of *Lapeirousia littoralis*, discussed above. The terminal taxon pairs are the same as in Figure 2A.

Bootstrap values (Fig. 1B) calculated with PAUP and based on a heuristic search with 100 replicates (Swofford, 1993) are drawn on the strict consensus tree obtained using Hennig86. Values above 70% are believed to have a 95% confidence level (Hillis & Bull, 1993). Values calculated for our trees range from 58% to 94%. The five terminal species pairs in the consensus tree have bootstrap values of 61% and higher. These values lend support to our speculations about evolution and speciation in terminal clades obtained by the cladistic analyses and allow us to frame hypotheses about the mechanisms of speciation in subgenus *Lapeirousia*. Ultimately we hope that the hypotheses about phylogenetic relationships presented here will be compared with phylogenetic reconstructions based on independent molecular methods of DNA sequencing or restriction enzyme analysis.

The phylogenetic analysis does not support our previous division of subgenus *Lapeirousia* into two sections (Goldblatt & Manning, 1990). In this classification species of section *Sophronia* fall in two major clades, those above nodes 2 and 6 (Fig. 1). Section *Lapeirousia*, however, corresponds to the clade above node 9. A preferable classification for the subgenus would be to restrict section *Sophronia* only to the species above node 2 and to recognize a third section for those at node 6, thus according sectional rank to the three major clades (Fig. 1) of the subgenus. A revised sectional classification based on our phylogenetic analysis will be included in a taxonomic revision of *Lapeirousia* currently in preparation.

SPECIATION MECHANISMS IN TERMINAL TAXA

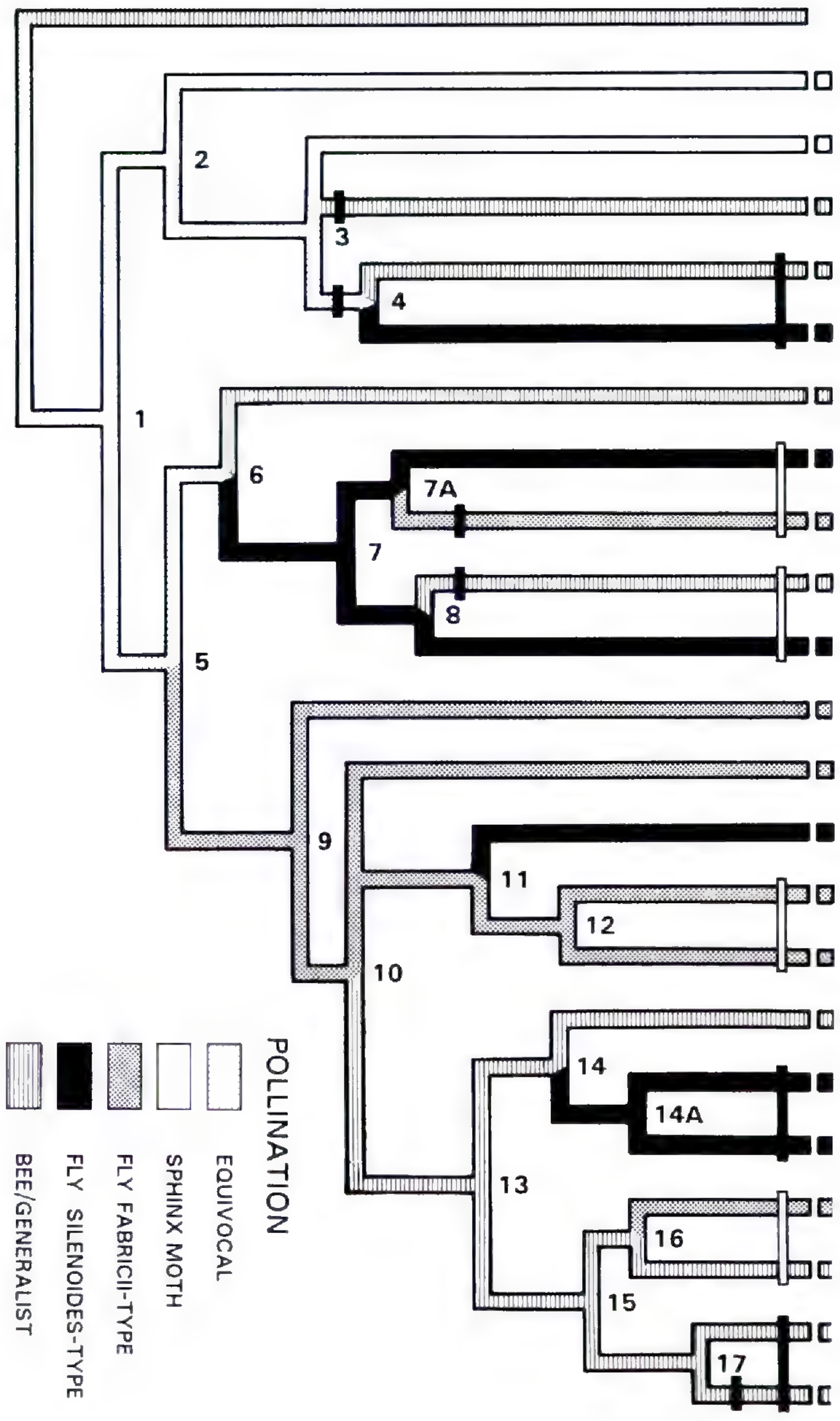
There are five terminal pairs (Fig. 2A: nodes 4, 8, 12, 16, and 17) available for analysis on the consensus tree obtained by successive weighting, and three of these are present on the unweighted consensus tree. The alternative hypothesis provides two more pairs (Fig. 2B: node 7A, 14A, the last one present in more than half of the most parsimonious trees). Moreover, these last two pairs are members of species trichotomies in the trees in which they are not terminal pairs. For analysis of biological differences, we compared the biology of the species at the terminal nodes to assess the factors that might have led to speciation of these pairs. The environmental determinants taken into account in this analysis are spatial separation, edaphic differences, and pollinator divergence (Table 2). There is no separation in flowering time between the species in any of the pairs available for analysis (Goldblatt et al., 1995).

Table 2. Distribution of differences (indicated by an asterisk, *) among taxa of terminal sister groups. Inferred differences in parentheses. 4 = *L. oreogena-montana*; 7A = *L. silenoides-verecunda*; 8 = subsp. *pyramidalis*-subsp. *regalis*; 12 = *L. macrospatha-arenicola*; 14A = *L. dolmitica-violacea*; 16 = *L. fabricii-barklyi*; 17 = *L. divaricata-spinosa*.

	Node						
	14A	4	7A	8	12	16	17
Allopatry	*	*	–	–	–	–	*
Parapatry	–	–	*	*	*	*	–
Soil type	*	–	*	*	–	*	*
Pollinator	–	*	(*)	*	(–)	*	–

A geographical component (Fig. 4) is present in all of the terminal pairs and the sister species are either allopatric, i.e., separated by a significant geographic distance (nodes 4, 14A, and 17), or parapatric, i.e., their ranges are adjacent although they do not grow intermixed (nodes 7A, 8, 12, and 16). In addition, members of most species pairs occur on a different soil type (nodes 7A, 8, 14A, 16, 17, but not those at nodes 4 and 12). Pollinator divergence characterizes three of the four parapatric species pairs (nodes 7A, 8, and 16) but only one of the allopatric pairs (node 4).

There are floral differences between the species in all the terminal pairs except at node 17 (*Lapeirousia divaricata* and *L. spinosa*). These differences are substantial at node 16 (*L. barklyi* and *L. fabricii*), involving morphology and markings, and accompany a shift in floral type and pollination syndrome between fly and bee pollination. Floral differences are less marked at nodes 4, 7A, 8, 12, and 14A and largely involve pigmentation and small changes in tube length. These relatively mi-



SPECIES	NUMBER *n*	SOIL TYPE	POLLINATOR
SUBGENUS PANICULATA			
LITTORALIS	8	KALAHARI SAND	(SPHINGIDAE)
ODORATISSIMA	8	KALAHARI SAND	(SPHINGIDAE)
PLICATA	8	KAROO CLAY	GENERALIST
MONTANA	8	DOLERITE CLAY	GENERALIST
OREOGENA	8	DOLERITE CLAY	NEMESTRINIDAE: *Pr.* SP. NOV.
EXILIS	9	QUARTZITE AND SAND	GENERALIST
SILENOIDES	9	NAMAQUA GRANITE	NEMESTRINIDAE: *Pr. per.*
VERECUNDA	9	MALMESBURY SHALE	(TABANIDAE/NEMESTRINIDAE)
P. PYRAMIDALIS	9	KAROO CLAY	SPHINGIDAE: *H. celerio*
P. REGALIS	9	STONY SANDSTONE	NEMESTRINIDAE: *Pr. per.*
ANCEPS	9	TMS SAND	TABANIDAE: *Ph. gulosa*/NEMESTRINIDAE: *M. longi.*
SIMULANS	?	KALAHARI SAND	(TABANIDAE)
JACQUINII	9	TMS SAND	NEMESTRINIDAE: *Pr.* SP. NOV. & *Pr. per.*
MACROSPATHA	?	KALAHARI SAND	(NEMESTRINIDAE: *M. longi.*)
ARENICOLA	8	KALAHARI SAND	(TABANIDAE)
TENUIS	?	SAND	(APOIDEA)
DOLOMITICA	8	QUARTZITIC SANDS	NEMESTRINIDAE: *Pr. per.*
VIOLACEA	8	TMS SAND	NEMESTRINIDAE: *Pr. per.*
FABRICII	8	TMS SAND	TABANIDAE: *Ph. gulosa*/Nemestrinidae: *M. longi.*
BARKLYI	8	KALAHARI SAND	FIDELIIDAE: *P. major*
DIVARICATA	?	SANDS	GENERALIST
SPINOSA	8	LIGHT CLAY	APOIDEA

nor differences in floral features either accompany a change in pollinator species within the same general pollination syndrome (fly pollination) (node 7A), or a shift between fly and generalist pollination (nodes 4, 8, and 16), or are not accompanied by shifts in pollinator at all (nodes 12 and 14A). Differences between the allopatric *L. divaricata* and *L. spinosa* (node 17) and the parapatric *L. arenicola* and *A. macrospatha* are mainly vegetative, and no change in pollination system is involved.

Speciation in subgenus *Lapeirousia,* as far as can be assessed by comparing the terminal pairs in the cladogram, thus appears to be exclusively geographic, either allopatric or parapatric. Speciation is usually combined with specialization for a different soil type, and a shift in pollinator typically accompanies the speciation event in three of the four parapatric pairs but not in allopatric pairs (Table 2). Significant changes in flower architecture accompany shifts between bee and fly pollination. Only minor or no floral changes at all occur in shifts within a single pollination system.

HISTORICAL ANALYSIS

There are three potential problems with the ecophylogenetic method for analyzing the evolutionary history of ecological features (Armbruster, 1992): stability of cladogram topology, completeness of ecological data, and circularity of reasoning. The reconstructed phylogeny of subgenus *Lapeirousia* is generally well supported (Fig. 1B), and the ecology of nearly all species is known (see Fig. 4). The edaphic hypothesis is free from the danger of circular reasoning because soil preferences were not used to reconstruct the phylogeny. There is, however, a possibility for circularity of reasoning regarding the evolution of pollination types because a number of floral characters of obvious adaptive value in pollination were used to generate the phylogeny. These are perianth tube length (character 13), perianth color (character 15), upper tepal orientation (character 18), and presence or absence of fragrance (character 23). In the absence of data independent of the ecological data being analyzed, Armbruster (1992) has suggested that the independence of characters used can be assessed a posteriori by checking for high consistency between the phylogeny and the ecological feature under consideration.

In subgenus *Lapeirousia* the phylogeny and pollination system are poorly correlated suggesting that there is no circular relationship between the two. The consistency indices for the four characters related to pollination type are 0.25, 0.16, 0.33, and 0.20, respectively. These are at the lower end of the scale for morphological characters (0.20 to 1), unrelated to pollination system, and also argue against any circularity in our analysis. Another challenging test of the ecophylogenetic hypothesis is to generate predictions based on the hypothesis and compare the predictions with new observations (Armbruster, 1992). In subgenus *Lapeirousia* our ecophylogenetic hypothesis includes the inference that the *L. silenoides*-type long-tongued fly pollination (Goldblatt et al., 1995) has evolved repeatedly. A prediction of this hypothesis is that the specialized corollas in these lineages differ from one another in detail, although they are functionally and superficially similar. This is indeed the case (see below). The ecophylogenetic hypothesis about evolution of pollination systems in subgenus *Lapeirousia* is thus supported by all three tests.

EDAPHIC DIVERSIFICATION

Species of subgenus *Lapeirousia* show nearly complete substrate fidelity. It is most parsimonious to assume that coarse and sandy soil in general (four changes) rather than fine clay (five changes) was the substrate favored by the species ancestral to subgenus *Lapeirousia,* although it is not possible to infer whether this was Kalahari sand or Table Mountain Series sand (Fig. 4). Comparison of the habitat and distribution of subgenus *Paniculata* (Goldblatt, 1990b) with those of subgenus *Lapeirousia* suggests the former. Ecological diversification to clay soils derived from shales or dolerite occurred within the clades defined by nodes 3 (*L. plicata, L. montana,* and *L. oreogena*), 7 (*L. verecunda* and *L. pyramidalis* subsp. *pyramidalis*), and 17 (*L. spinosa*). A single species, *L. silenoides* (node

←

Figure 4. Pollinators, chromosome numbers, soil types, and patterns of allopatry plotted on the historical hypothesis for the evolution of pollination systems in subgenus *Lapeirousia,* derived from the cladogram shown in Figure 2. Long solid bars indicate allopatry; long hollow bars, parapatry; short solid bars, colonization of clay substrates. Pollinators indicated in parentheses are inferred on the basis of floral morphology as detailed by Goldblatt et al. (1995). Pollinator names have been abbreviated as follows: *H.* = *Hippotion* (Lepidoptera: Sphingidae), *P.* = *Parafidelia* (Hymenoptera: Fideliidae), *Ph.* = *Philoliche* (Diptera: Tabanidae), *Pr.* = *Prosoeca* (Diptera: Nemestrinidae), *M. longi.* = *Moegistorhynchus longirostris* (Diptera: Nemestrinidae).

7A), is virtually restricted to Namaqualand granite and granitic sands. Edaphic divergence characterizes five of the seven terminal species pairs and is likely to have provided the initial impetus for genetic differentiation between founder and parent populations.

DIVERSIFICATION OF POLLINATION TYPES

A well-developed floral tube and pale flower appear to be ancestral in the subgenus, and pollination by long-tongued insects may be inferred to be plesiomorphic. The outgroup, subgenus *Paniculata*, is diverse in floral morphology (Goldblatt, 1990b), but the floral types present in subgenus *Paniculata*, coupled with field observations (Goldblatt et al., 1995), suggest that pollination by bees or a combination of bees and Lepidoptera is predominant. Just three species in subgenus *Paniculata* have extremely long floral tubes and display some of the same characteristics as species in subgenus *Lapeirousia* that are known to be pollinated by sphinx moths or long-tongued flies. These species are, however, all believed to be derived in subgenus *Paniculata*, not only because of their derived floral characters but because of their apomorphic karyotypes (Goldblatt & Takei, 1993). Hence, the inference is strong that although both moth and fly pollination are present in the outgroup at low frequencies, these pollination types are independently derived within each of the subgenera.

In subgenus *Lapeirousia*, species richness is not a function of any one pollination strategy. Each of the major clades includes a diversity of pollination systems, and shifts in pollination system have occurred repeatedly. A pale flower (sphinx moth- and *L. fabricii*-type flowers) is evidently plesiomorphic at nodes 4, 6, and 9 (Fig. 4). The inference follows that the *L. silenoides*-type fly pollination (involving *Prosoeca peringueyi* and *P.* sp.), associated with vividly pigmented flowers, was derived four times in the subgenus, at node 4 (*L. oreogena*), node 7A (*L. pyramidalis* subsp. *regalis* and *L. silenoides*), node 14A (*L. dolomitica* and *L. violacea*), and node 11 (*L. jacquinii*). The *L. fabricii*-type fly pollination (involving *Moegistorhynchus longirostris* and *Philoliche gulosa*) is inferred to have been independently derived three times within the subgenus, at node 7A (*L. verecunda*), and twice in the entire clade at node 9 (Fig. 4). It is most parsimonious to infer a shift to a generalist or bee-dominated system at node 13. In this scenario, a reversal to the *L. fabricii*-type fly pollination system occurred at node 16 (the *L. silenoides*-type fly pollination system evolved at node 14 of the clade). The *L. fabricii*-type fly pollination appears to be the ancestral pollination system for more than half the species in the subgenus (the entire clade defined by node 9). Bee/generalist pollination appears to be the most derived pollination state in the clade defined by node 9.

Thus, it appears that most of the pollination types found in subgenus *Lapeirousia* have evolved more than once. Bee or generalist pollination has evolved four or five times (node 3 or both nodes 3 and 4, and nodes 6, 8, and 10), *L. fabricii*-type fly pollination three times (nodes 5, 7A, and 16), *L. silenoides*-type fly pollination four times (nodes 4, 6, 11, and 14), and sphinx moth pollination once or twice (nodes 2 or 3 or both). Pollination systems in subgenus *Lapeirousia* are thus evolutionarily labile and prone to parallel evolution and reversal. This applies equally to shifts between bee and fly systems and to shifts between the two fly systems.

The evolution of floral actinomorphy in subgenus *Lapeirousia* coincides with the evolution of an acaulescent habit. Floral actinomorphy is restricted to the species at node 3, all of which are of low stature with a tufted, acaulescent habit. Except for *L. odoratissima* these species grow on clay, and the colonization of more stable clay soils by the ancestor(s) of the remaining species in the clade may have facilitated the diversification of plants with this growth form. Acaulescence has the advantage of retaining the ovules and developing seeds at or below soil level, thus providing protection from the weather and predators (Burtt, 1970). The tufted growth form favors vertical flower presentation, and floral actinomorphy is a likely result. A long floral tube enables the flowers to project above the leaf and bracts. The development of long-tubed actinomorphic flowers in subgenus *Lapeirousia* is thus most likely related to plant habit and floral presentation and not to pollinator-driven selection.

Discussion

Our analysis suggests that for the terminal species pairs in subgenus *Lapeirousia* speciation has been exclusively at the diploid level and has mostly involved a combination of shifts in substrate preferences when descendant species occur in adjacent habitats or geographic isolation when the descendant species are separated by significant distance and may or may not occur on different substrates. For the species analyzed the former situation slightly predominates. This pattern is consistent with the hypothesis (Goldblatt, 1978; Linder, 1985; Cowling & Holmes, 1992) that edaphic differences are the predominant cause of species richness in the south-

western part of southern Africa. The isolating effect of discontinuities in substrates (e.g., Kruckeberg, 1986) may in fact be the most significant cause of local and taxonomic diversity. It has been suggested by Linder and Vlok (1991) that each distinctive habitat may represent a "geographic"" region without the usual physical barriers associated with allopatric speciation. Such microgeographic or parapatric speciation is particularly likely in the southwestern part of southern Africa where varied soils and topography accompanied by steep precipitation gradients provide a strong selection differential for population divergence and the development of edaphically isolated populations (Goldblatt, 1978; Linder, 1985).

Local divergence between populations, whether linked to edaphic specialization or not, is possible only if gene flow is sufficiently restricted to permit genetic differentiation either by drift or selection. Limited gene flow is typical of most Iridaceae (Goldblatt, 1991), and short gene dispersal distances are a characteristic of most plants in the southwestern part of southern Africa (Cowling et al., 1992). The effect of restricted gene flow is that neighboring populations may be well defined as a result of selective differentials or random drift (Levin, 1981, 1993).

Speciation in subgenus *Lapeirousia* seems to have been initiated by shifts in substrate preference. This has in most instances been accompanied by changes in floral morphology and shifts in pollination strategy, thereby enhancing genetic differentiation initiated by adaptation to different substrates. Edaphic differences in Namaqualand and the northwestern Cape are often associated with other physical differences such as altitude, aspect, and rainfall. They thus signify more profound niche differences than might be suggested by edaphic differences alone. The action of selection on founder populations on novel substrates should be correspondingly stimulated, and would enhance small-scale genetic differentiation. We anticipate that strong selective pressure for the development of prepollination isolating mechanisms would follow the development of these edaphically adapted genotypes at the contact zones between the parent and daughter populations.

In other genera of Iridaceae and some Orchidaceae and Amaryllidaceae small changes in color and scent are sufficient to attract different pollinators and prevent hybridization (Johnson, 1992; Johnson & Bond, 1994; Paulus & Gack, 1990; Steiner et al., 1994). In subgenus *Lapeirousia* the floral changes necessary for a shift between pollination by sphinx moths and long-tongued flies or between the two types of long-tongued fly pollination primarily involve perianth pigmentation, while those necessary for a shift to bee pollination involve a shortening of the floral tube and sometimes a change in flower color. Both flower color and flower shape are frequently governed by rather simple genetic systems (Gottlieb, 1984; Macnair, 1989). A shorter floral tube is readily achieved through paedomorphosis, while simple heterochronic changes in development may account for other observed floral differences (Guerrant, 1982). In *Aquilegia,* for instance, many of the differences in shape that lead to the attraction of different pollinators are governed by small numbers of genes (Prazmo, 1965).

For the species of subgenus *Lapeirousia* relatively simple mutational or recombinational events might result in a change in flower color from cream to magenta or violet (or vice versa), instantly shifting the plant into a different pollinator guild and effectively isolating it from the parent species. Potentially nonadaptive bottlenecks between pollination systems are thus likely to be small, and pollinator-directed selection for differences in floral morphology should be rapid. This is particularly significant in a situation where floral conformity is as strongly stressed as in the long-tongued fly guilds (Manning & Goldblatt, 1996). Although shifts in pollination system in subgenus *Lapeirousia* involve a complete change in the pollinator species, there can be occasional overlap. For example, we have seen long-tongued fly species visiting short-tubed flowers and some bees occasionally collect pollen from long-tubed species, which they may successfully pollinate. In addition, *Prosoeca peringueyi* has been observed visiting a few individuals of *L. verecunda* at the single known site where the ranges of this species and *L. silenoides* meet. It is thus possible that shifts between the various pollination systems could have occurred with intermediate phases in which both old and new systems operated. Because of the apparently small morphological/genetic changes required for shifts between the various pollination systems in subgenus *Lapeirousia,* the shifts are likely to have been rapid.

We postulate that a source of strong differential selection for the incipient species to develop specific pollination systems was provided by preexisting and independently established pollination guilds involving long-tongued flies in the families Nemestrinidae and Tabanidae. An increase in tube length would enable a generalist species to enter one of these guilds by excluding insects with shorter tongues from competing for nectar resources. A

decrease in tube length would facilitate the development of a generalist or bee-dominated pollination system. Shifts between the two long-tongued fly pollination systems require only a change in flower color, and plant species can thus shift readily between them. The minor morphological changes required to accomplish a shift between these pollination systems seem to have permitted rapid establishment of reproductive isolation between the diverging populations. Early stages in floral divergence by pollinator-directed disruptive selection are evident in *L. pyramidalis*. The two subspecies are characterized by differences in floral morphology (scent, flower color, tube length), which, although minor, enable them utilize different pollination systems.

Although prepollination isolating mechanisms include seasonal and habitat differences, as well as the use of different pollinators or different body parts of the same pollinator (Levin, 1978), separation in flowering period between related species pairs has not developed in subgenus *Lapeirousia*. This is probably due to the short rainy season and hence short period for biological activity for most organisms in western southern Africa.

Species of subgenus *Lapeirousia* with the same flower type and which belong to the same pollination guild rarely co-occur. In the few instances where two species with flowers of the same general type grow together (e.g., *L. jacquinii* and *L. violacea*; *L. fabricii* and *L. anceps*), the two differ in their chromosome number and no hybrids have been located (Goldblatt et al., 1995). We suggest that one consequence of this genetic isolation was that the genotype of populations colonizing new habitats would not be swamped by neighboring populations with a different chromosome number even in the absence of different pollination systems. A decrease in chromosome number characterizes the clades defined by nodes 2 and 13. These clades may thus represent repeated bursts of parallel radiation from founder species that had become genetically isolated from the ancestral stock.

Despite marked differences in floral morphology between closely related species in subgenus *Lapeirousia*, comparisons of biological differences within species pairs in the subgenus indicate that the diversity of flower types and pollination strategies occurred *after* the differentiation of local populations to new habitats. We hope that the hypotheses about phylogenetic relationships presented here will be compared with phylogenetic reconstructions based on independent molecular methods of DNA sequencing or restriction enzyme analysis.

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Appendix. Character states and character polarization. The outgroup for character polarization is *Lapeirousia* subg. *Paniculata*. For character 25, used in a secondary analysis (Fig. 3), the outgroup is *Savannosiphon*.

1. On the basis of outgroup comparison the woody corm tunics of subgenus *Lapeirousia* are apomorphic (1). Corm tunics of densely compacted fibers are characteristic of subgenus *Paniculata* (and of the related genera *Thereianthus* and *Micranthus*) (Goldblatt & Manning, 1990).

2. Entire to lobed corm bases characterize the species of subgenus *Paniculata* and several in subgenus *Lapeirousia*. Minutely serrated (denticulate) tunic bases occur in a number of species (Goldblatt, 1972), and the development of short spines (short-dentate) occurs in *L. divaricata* and its close ally *L. spinosa*, while *L. dolomitica*, *L. violacea*, and *L. tenuis* have long spines extending from the corm bases. The nature of the corm bases is treated as a multistate character with denticulate scored as (1), short-dentate as (2), and long-dentate as (3). The degree of serration, minutely toothed to short- or long-dentate, is regarded as additive and hence ordered.

3. Campanulate-shaped corms occur in all species of subgenus *Paniculata* and are regarded as plesiomorphic. Apomorphic broadly conic corms are found in three species of subgenus *Lapeirousia*, *L. tenuis*, *L. dolomitica*, and *L. violacea*.

4. The plesiomorphic condition in subgenus *Paniculata* is probably an actinomorphic flower (Goldblatt & Manning, 1990; Goldblatt & Takei, 1993), but we are sufficiently uncertain about the state in the outgroup that we prefer to score the character as (?). Most species of subgenus *Lapeirousia* have zygomorphic flowers, but four species that also have the aerial stem reduced (thus acaulescent) have actinomorphic flowers. Elsewhere the actinomorphic flower has been interpreted as a reversal from the zygomorphic condition, attendant on the acaulescent habit (Goldblatt, 1972, 1990b).

5. The acaulescent habit and densely tufted growth habit characterize four species of subgenus *Lapeirousia* (Goldblatt, 1972, 1990b). In these species the habit is constant irrespective of rainfall and other environmental conditions. Species such as *L. silenoides* are acaulescent under adverse conditions, and even *L. exilis*, normally acaulescent, will develop aerial stems under optimal conditions. The acaulescent growth form is unknown in subgenus *Paniculata* or in any other genus of tribe Watsonieae and must be regarded as apomorphic.

6. The seed surface cells in subgenus *Paniculata* and the closely related genus *Savannosiphon*, possibly the sister genus to *Lapeirousia* (Goldblatt, 1989), are lightly and irregularly colliculate-foveate and the cells are not arranged in regular files (Goldblatt & Manning, 1992). In subgenus *Lapeirousia* most species have seed surface cells in straight files and the epidermal cells are often strongly and regularly colliculate, scored as (1), or tuberculate, scored as (2), both presumably derived states. The patterning is such that species can immediately be placed in groups according to seed surface. A few species of subgenus *Lapeirousia* have the plesiomorphic seed surface type (see data matrix). Both subspecies *pyramidalis* and subspecies *regalis* are scored as having the tuberculate condition. Seed surface cells of *L. fabricii* are also sometimes weakly tuberculate but are more often colliculate, and the species is scored as having the colliculate pattern (alternate scoring produced no change in the topology of the strict consensus tree but it is one step longer).

It may be argued that the irregular or regular ordering

of cells in files and the surface sculpturing are separate characters, but they are fully correlated, and hence we prefer to treat them as a single one. The extent to which the surface cell wall is raised, either moderately (colliculate), or strongly, especially toward the center (tuberculate), is regarded as additive and hence this multistate character is ordered.

7. Seeds with primary surface sculpturing are rare in *Lapeirousia*, and seeds in subgenus *Paniculata* are globose, the plesiomorphic condition, except in *L. otaviensis* R. Foster and *L. neglecta* Goldblatt & Manning, which have seeds with a ruminate primary sculpturing (unpublished data). In subgenus *Lapeirousia* the seed surface is ridged in a diffuse ruminate pattern in *L. plicata* and *L. odoratissima*, scored as (1), and has a reticulate pattern in *L. oreogena* and *L. montana*, scored as (2). The character states are treated as additive with the diffuse pattern seen as a less specialized type of sculpturing than the very regular reticulate pattern.

8. Strongly developed winglike ridges are present on the locular sutures of the capsules of *Lapeirousia silenoides*, *L. verecunda*, and *L. pyramidalis*. These are regarded as apomorphic, being absent in the outgroup and in other species of subgenus *Lapeirousia*. Likewise, the development of auriculate lobes above the locules on the capsules of *L. arenicola* and *L. macrospatha* must be regarded as derived. Winglike ridges are scored as (1) and auricular lobes as (2), and the character is treated as unordered.

9. Production of branches mostly or entirely near ground level is characteristic of a few species of subgenus *Lapeirousia*, including *L. jacquinii*, *L. pyramidalis*, *L. silenoides*, and *L. verecunda*, and is regarded as derived. The plesiomorphic condition, branching of the flowering stem above ground level, occurs in all species of subgenus *Paniculata* and several of subgenus *Lapeirousia*. The acaulescent species all branch from the base by default because the aboveground internodes are contracted.

10. Geniculate lower tepals (with a sharp bend near the midline) are treated as apomorphic. In *Lapeirousia* the character is restricted to a handful of species of subgenus *Lapeirousia* and is not known at all in subgenus *Paniculata*, in which the lower tepals are straight or cupped.

11. Plicately ribbed leaves are apomorphic for subgenus *Lapeirousia* (Goldblatt & Manning, 1990). The plesiomorphic condition for *Lapeirousia* is a plane leaf. A few species of subgenus *Paniculata* have terete leaves, a secondary condition.

12. Firm-textured floral bracts are characteristic of the species of subgenus *Lapeirousia* and contrast with the soft-textured bracts of section *Paniculata*. Firm-textured bracts also occur in section *Fastigiata* of subgenus *Paniculata*, and appear to be derived here. Based on outgroup comparison, the firm-textured bracts of subgenus *Lapeirousia* are regarded as derived.

13. The perianth tube is shorter to about as long as the tepals in most species of subgenus *Paniculata*, and this is assumed to be the plesiomorphic condition. A tube longer than the tepals is regarded as apomorphic; a tube shorter than the tepals is scored as (1); a tube slightly longer, to 2–3 times as long as the tepals is scored as (2); a tube (3–)4–6 times as long as the tepals is scored as (3).

14. The development of a perianth tube with an abruptly widened throat or gullet is restricted to a few species of subgenus *Lapeirousia* (*L. fabricii*, *L. barklyi*, *L. divaricata*, *L. spinosa*). Species of subgenus *Paniculata* mostly have a uniformly cylindrical tube, sometimes gradually widened toward the apex, or a widely funnel-shaped tube. Based on outgroup comparison we assume the gullet in subgenus *Lapeirousia* to be derived. A widely funnel-shaped tube (present in the actinomorphic-flowered *L. avasmontana*) may be the plesiomorphic state for *Lapeirousia*, and is scored as (0). The more or less cylindrical tube of the zygomorphic-flowered species of subgenus *Paniculata*, as well as in most species of subgenus *Lapeirousia*, is scored as (1) and the presence of a gullet as (2). The character is treated as ordered as we regard the trend in the elaboration of the tube as additive.

15. The predominant perianth color in the outgroup, subgenus *Paniculata*, is blue with white markings outlined in dark blue to purple and is regarded as the plesiomorphic condition. Other colors are scored as follows: predominantly white, sometimes with blue or mauve markings and/or a lilac flush on the reverse of the tepals (1); white to cream to ivory with red markings on the lower tepals, and on the reverse of the tube and sometimes of the tepals (2); shades of dark red to purple or violet to blue, in either case with contrasting white markings (3). The character states are unordered.

16. Based on outgroup comparison the more or less spathulate tepals of *Lapeirousia silenoides*, *L. verecunda*, and *L. exilis* are apomorphic. The plesiomorphic condition, ovate to lanceolate tepals, characterizes the species of subgenus *Paniculata* and the other species of subgenus *Lapeirousia*.

17. The development of a tooth or ridge of raised tissue at or near the base of each of the lower tepals is an unusual character and, based on outgroup comparison, derived. Filiform teeth occur in *Lapeirousia anceps*, *L. fabricii*, *L. simulans*, *L. macrospatha*, and are weakly developed in *L. jacquinii*. Ridged teeth occur in *L. divaricata*, *L. spinosa*, and *L. barklyi*. We assume these structures are homologous and represent two states of the same character; filiform teeth are scored (1), and ridged teeth as (2).

18. Erect to arched upper tepals, restricted to a few species of subgenus *Lapeirousia*, are regarded as derived. Species of subgenus *Paniculata* and many of subgenus *Lapeirousia* have all the tepals extended and lying in more or less the same plane.

19. Bracts strongly folded in the midline or keeled, present in several species of subgenus *Lapeirousia*, are treated as derived; the bracts of subgenus *Paniculata* are neither folded nor keeled.

20. The inner floral bracts are about as long as to slightly shorter (but narrower) than the outer bracts in all species of the outgroup. Species of subgenus *Lapeirousia* always have the inner bracts about half as long as the outer or less, hence are regarded as apomorphic for the character.

21. Small to moderate sized flowers (excluding the perianth tube) are most likely plesiomorphic for the outgroup (upper tepal less than 18 mm long). A few species of subgenus *Lapeirousia*, notably *L. fabricii* and *L. barklyi*, have notably larger flowers, the upper tepals being 18–27 mm long, a condition regarded as apomorphic.

22. Strongly obtuse to retuse bracts are a feature of two taxa of subgenus *Lapeirousia*, *L. pyramidalis* subsp. *pyramidalis* and *L. pyramidalis* subsp. *regalis*, and the condition is regarded as apomorphic. Bracts are acute in other species of the subgenus and in subgenus *Paniculata*.

23. Scented flowers of, for example, *L. pyramidalis* subsp. *pyramidalis*, *L. divaricata*, and *L. odoratissima* are regarded as derived. Scented flowers are rare in subgenus

Paniculata and are apomorphic within the subgenus. There is no information available about scent chemistry in *Lapeirousia*, and although scents may differ in subgenus *Lapeirousia* we simply score presence or absence of any scent.

24. In subgenus *Paniculata* (and most species of subg. *Lapeirousia*) the lower and upper lateral tepals separate from the tube at about the same level, the plesiomorphic condition. In *L. divaricata* and *L. spinosa* the lower and upper lateral tepals are united for 3–5 mm, apomorphic for these two species.

25. For the analysis with *Savannosiphon* as outgroup. Corms with flat bases are unique in Iridaceae to *Lapeirousia* and thus scored as apomorphic (1).

PHYLOGENETIC RELATIONSHIPS, SEED CHARACTERS, AND DISPERSAL SYSTEM EVOLUTION IN AMARYLLIDEAE (AMARYLLIDACEAE)[1]

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Abstract

The phylogeny of the mostly African tribe Amaryllideae is presented as a basis for classification and an enquiry into the evolutionary interrelationship between seed and fruit characters and seed dispersal modes. The cladistic analysis is based on morphological, seed anatomical, and cytological data, of which seed and fruit specializations are illustrated. Three dispersal modes, anemochory, atelechory/rain wash, and autochory, are optimized onto the selected cladogram and the pattern is considered in terms of functional fruit and seed morphology. The new classification recognizes two monophyletic subtribes: Crininae (*Boophone* sensu stricto, *Crinum*, *Ammocharis*, and *Cybistetes*) and Amaryllidinae (*Amaryllis*, *Nerine*, *Brunsvigia*, *Crossyne*, *Hessea*, *Strumaria*, and *Carpolyza*). The phylogeny suggests that in Amaryllidinae the ability of the green, stomatose seeds to mature after they are released favored the development of rapidly shed, wind-tumbled infructescences in three clades especially in semiarid, southwestern Africa. In Crininae the seeds are large, cork-covered, endosperm-rich, and relatively slow developing. The limited seed dispersal mode in *Crinum* and *Ammocharis* appears to be a consequence of the derived indehiscent fruit, which is basal in Crininae, and the anchoring function of their persistent, lax scape.

Amaryllideae, a monophyletic group consisting of 11 currently recognized genera and approximately 155 species, is one of nine tribes (sensu Dahlgren et al., 1985) in the monocotyledonous family Amaryllidaceae. The members are all bulbous herbs with distichous or rarely rosulate leaves and a lateral, solid, naked scape which is terminated by an umbel-like cluster of flowers. Their seeds are characteristically large and nondormant. Although remarkably uniform in floral and vegetative morphology, much diversity exists in the tribe's fruiting structures, some of which function as specialized units of dispersal in wind or water. Members of the tribe inhabit grassland, savanna, and tropical forests in sub-Saharan Africa, but are most speciose in southern Africa, where habitats include semiarid, dwarf shrublands in a winter-rainfall climate. The tribe's only pantropical representative is *Crinum* L., which extends from Africa to Madagascar, the Mascarene and Pacific Islands, and the tropics of America, Asia, and Australia.

Several Amaryllideae have traditional and economic uses. The charred and crushed bulb scales of *Ammocharis coranica* (Ker Gawl.) Herb. have been used as an adhesive (Phillips, 1917, 1938), and a decoction of the bulbs of *Boophone* Herb., *Brunsvigia* Heist., *Crinum*, and *Nerine* Herb. have provided medicine and poison to many African people (Phillips, 1917; Watt & Breyer-Brandwijk, 1962). The use of the highly toxic bulbs of *Boophone disticha* (L.f.) Herb. for arrow poison by early hunter-gatherers has been particularly well documented (Bradlow, 1994; Forbes, 1986; Forbes & Rourke, 1980). Numerous forms and hybrids of *Nerine*, *Amaryllis* L., and *Crinum* are cultivated for their elegant flowers, and the spherical fruiting heads of *Boophone* and *Brunsvigia* are locally gathered for dried floral arrangements.

Amaryllideae were first delimited as monophyletic by Traub (1965, 1970), who recognized the presence of threadlike "fibres" in torn-off leaves and bulb scales as diagnostic for the tribe (character 1). This feature has since been corroborated by four non-homoplasious synapomorphies: uniteg-

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Table 1. Major recent classifications of Amaryllideae.

	Crinum, Ammocharis, Cybistetes, Boophone	*Amaryllis, Nerine, Brunsvigia*	*Hessea, Carpolyza, Strumaria*	*Crossyne*
Traub (1957)	Crininae	Crininae	Strumariinae	
Traub (1962)	Crineae	Crineae	Hesseae	
Traub (1963)	Crineae	Crineae	Strumarieae	
Traub (1965, 1970)	Crineae	Crineae	Crineae	
Dahlgren et al. (1985)	Amaryllideae	Amaryllideae	Amaryllideae	
D. & U. Müller-Doblies (1985)	Crininae	Crininae	Strumariinae	
Snijman & Linder	Crininae	Amaryllidinae	Amaryllidinae	Amaryllidinae

mic ovules (Huber, 1969) and bisulculate pollen grains (Schulze, 1984) with spinulose exine sculpturing (Meerow, 1995), to which we add green embryos in nondormant, water-rich seeds (character 33).

Various subtribal classifications of Amaryllideae have been proposed (Table 1), most of which reflect the nomenclatural confusion introduced by Traub's (1957, 1962, 1963, 1965, 1970) continuous misapplication of the name *Amaryllis* to the unrelated genus *Hippeastrum* Herb. (Brummit, 1987). These systems differ only in the rank attributed to the two subtribal groups recognized in Amaryllideae (Crineae *sensu* Traub, 1965, 1970). Thus far, the relationships of the genera within these groups have never been disputed.

Amaryllidinae (Pax, 1887) or Crininae (Traub, 1957, 1963), the larger of the two subtribes, are characterized by the presence of minute "fibres" between the broken parts of leaves and bulb scales, a solid scape, and regular to zygomorphic flowers (Traub, 1963). Strumariinae, which are defined by no single character but by a combination of characters, comprise small plants with mostly two leaves surrounded by an amplexicaul cataphyll; regular flowers with a reduced perigone tube; filaments inserted into a sheath formed by the anther connective; and style variously connate to the filaments (Müller-Doblies, 1985).

Essentially these interpretations were limited to basic vegetative and floral morphological data and they were phenetically based; therefore the monophyly of the subtribal groups was never explicitly questioned.

The primary aim of this study was to use new morphological data from the infructescences, capsules, and seeds of Amaryllideae in a phylogenetic analysis to establish monophyletic groups of genera, and to assess the monophyly of the traditionally recognized subtribes Amaryllidinae and Strumariinae. Of special interest in Amaryllideae are the unique and complex seed dispersal mechanisms by wind or water. To analyze the evolution of these dispersal mechanisms, changes in seed and fruit characters are traced on the phylogenetic tree to assess whether the different dispersal modes may have been facilitated by these functionally related characters. Lastly, in an attempt to establish evolutionary patterns in the ecology of Amaryllideae, we use the phylogeny to analyze the interrelationships between seed and fruit characters, dispersal traits, phenology, and phytogeography.

Materials and Methods

Character Analysis

Morphological data on *Ammocharis* Herb., *Brunsvigia, Crinum,* and *Nerine* were obtained from the literature, living collections at Kirstenbosch National Botanical Garden, and dried material at NBG. *Crinum variabile* (Jacq.) Herb. and all species of *Amaryllis, Boophone, Crossyne* Salisb., *Carpolyza* Salisb., *Cybistetes* Milne-Redh. & Schweick., *Hessea* Herb., and *Strumaria* Jacq. were studied in the field, and the South African summer-rainfall representatives of *Crinum* and *Ammocharis* were studied in cultivation.

Leaves, flowers, and seeds for anatomical study were fixed in FAA (90 ml 70% ethanol; 5 ml glacial acetic acid; 5 ml formaldehyde), subsequently dehydrated in an ethanol-toluene series, embedded in wax, and cut with a rotary microtome at 10–15 μm. Sections were stained with safranin and alcian blue, and photographed with a Zeiss Axioskop. Seeds examined by scanning electron microscopy were fixed in FAA, dehydrated in ethanol, and critical point dried before sputter-coating with Au/Pd. Photographs were taken with a Cambridge S200 SEM at 10 kV. Documentation for the taxa studied micromorphologically is given in Appendix I. The micromorphological characters reported here for *C. variabile* conform to published results of other African, Asian, and Australian species of the genus (Dutt, 1962, 1970; Howell & Prakash, 1990; Merry,

Table 2. Distribution of character states among the genera of Amaryllideae and subgenera of *Hessea* and *Strumaria*. Indeterminate states are coded as "?".

Haemantheae	00000	00000	00000	00000	00000	00000	0000
Crinum	10100	00100	?0000	11100	10011	10000	1110
Ammocharis	11100	00100	00000	11000	10011	10000	1110
Cybistetes	11100	00100	00000	11100	12011	10000	1110
Boophone	10000	00000	00000	11000	10111	00000	1110
Amaryllis	10000	00000	11000	11100	10000	00000	0010
Nerine	10000	00000	12000	11100	11000	00111	0010
Brunsvigia	11000	01010	12000	11100	12000	00111	0010
Crossyne	11001	01210	?2000	11100	12000	00111	0010
Hessea subg. *Hessea*	10010	00011	02002	11000	12000	00111	0010
Hessea subg. *Namaquanula*	10010	00011	01101	11000	12000	00111	0010
Hessea subg. *Kamiesbergia*	10010	00011	0201?	11000	12000	00111	0010
Strumaria subg. *Strumaria*	10000	00000	00000	11011	10000	00111	0011
Strumaria subg. *Tedingea*	100?0	00010	00000	11011	11000	00111	001?
Strumaria subg. *Gemmaria*	10010	100?0	00001	11011	12000	00111	0011
Carpolyza	10000	00010	00001	11001	11000	00111	0011

1937; Toilliez-Genoud, 1965; Venkateswarlu & Lakshmi, 1978). New seed data are provided for *Boophone*, *Ammocharis*, *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria*.

Of the 34 morphological characters identified for the phylogenetic analysis, 5 have slightly overlapping states: leaf number, pedicel length, anther attachment, staminal tube length, and scape habit after seed set. The sets of different states recognized in these characters nevertheless proved to be informative, since the topology was considerably less resolved when they were excluded from the phylogenetic analyses. Only one of the four multistate characters was treated as unordered. Autapomorphies were excluded from the cladistic analyses but were later inserted onto the cladograms. Character state distribution is provided in Table 2.

CLADISTIC ANALYSIS

Cladistic analyses were carried out using the implicit enumeration (ie*) option of Hennig86 (Farris, 1988), and the tree bisection reconnection (TBR) branch swapping of PAUP (Swofford, 1993). Trees were rooted by designating an outgroup (Nixon & Carpenter, 1993). Anderberg and Tehler (1990) suggested that for taxonomic studies only strict consensus trees, containing only components retrieved by each of the complete set of most parsimonious trees, should be used. This is a very conservative approach, as these consensus trees are substantially less informative than the most parsimonious trees on which they are based (Farris, 1983), and they reveal little about process, as in character state change (West & Faith, 1990). Carpenter (1988) therefore argues that one of the most parsimonious cladograms should be preferred over a consensus tree as a phylogenetic hypothesis. To choose among the set of most parsimonious trees, we use the logic that adding to the potential homoplasy of a character which is already highly homoplasious should not be as significant as adding to the potential homoplasy of an otherwise non-homoplasious character. Consequently, we select those topologies from the set of most parsimonious trees that minimize the possible homoplasy of the least homoplasious characters. There are several approaches by which this logic can be implemented. Goloboff (1993) developed a method for simultaneously downweighting homoplasious characters and locating parsimonious trees, but this has been criticized by Turner (1995). Meacham (1994) proposed a method for calculating the character compatibilities in a data set, and weighting those characters that are maximally compatible. We used the successive approximations weighting scheme implemented in Hennig86 using the rescaled consistency index: the product of the character consistency index and the character retention index (Farris, 1969; Carpenter, 1988). Maximally homoplasious characters, if they occur in only two taxa, would have a consistency index (CI) of 0.5, a rescaled consistency index of 0, and a weight of 0. Minimally homoplasious characters, with CI = 1 and retention index (RI) = 1, would have a rescaled consistency index of 1 and a weight of 10. In extreme cases Goloboff (1991a, b) has questioned the validity of using the rescaled consistency index as a measure for deciding which most parsimonious cladogram is to be preferred. Despite these reservations, successive approximations weighting analysis is considered to have value when used with caution (Crisp & Weston, 1995). Our preferred most parsimonious tree was com-

pared with the majority rule tree and the strict consensus tree, and decay analysis (Bremer, 1988; Donoghue et al., 1992) was conducted to provide measures of strength for the phylogenetic hypothesis represented by the most parsimonious tree topology. To investigate alternative hypotheses of monophyly, the additional cost of grouping *Amaryllis* within the *Boophone* clade was determined using MacClade (Maddison & Maddison, 1987). Character distributions on cladograms were examined, and figures were generated using CLADOS (Nixon, 1992).

To analyze the number of times a particular dispersal mode evolved and to determine its interrelationship with fruit, seed, and phenology states in the lineage, the dispersal modes and phenological states were plotted on the terminal taxa of the cladogram and the most parsimonious interpretation of the character states at each inner node was obtained using Farris optimization (Farris, 1970; Mickevich, 1982). The states coded for seed dispersal are taken from Van der Pijl (1982): anemochory (wind dispersal), which is divided into anemogeochory (tumbling) and anemoballists (wind ballists); atelechory (limited dispersal); and autochory (dispersal by the plant itself), which is used here in the passive sense. For the analysis of plant phenology, the foliage leaves were coded as synanthous (the leafing period coincides with the flowering period) or hysteranthous (the leafing period is separated from the flowering period).

All known seed and fruit characteristics were included in the data matrix for phylogeny construction, but for the analysis of dispersal mode only the abscission of the infructescence (character 22) was used. Following Deleporte (1993), the primary coding of such a character may not necessarily introduce circularity into our interpretation of dispersal system evolution.

CHARACTER CODING

The weightings determined by the successive approximations character weighting routine are given in parentheses and autapomorphies are marked with an asterisk.

1. (10) *Bulb scales*: without extensible elements when pulled = 0, with numerous extensible elements when pulled = 1.

Although Traub (1965, 1970) stated that "fibres" appear when the bulb scales and leaves of Amaryllideae are torn apart, an unpublished report (P. Goldblatt, pers. comm.) that these highly extensible elements are long, spirally thickened tracheids is shown to be correct. Before elongation the tracheids are ca. 325 μm long and at all stages the wall thickenings are characteristically lightly stained by safranin. When artificially stretched the cottony appearance of these elements is reliably diagnostic for the tribe.

2. (3) *Outermost bulb scales*: fleshy to parchment-like = 0, hard and brittle = 1.

In the outgroup and most representatives of Amaryllideae, the outer tunics form brown, softly fibrous coverings. Bulbs with extremely thick coverings, which become hard and brittle, are found in *Ammocharis, Cybistetes, Crossyne,* and the *Brunsvigia* species with prostrate leaves. Although the chemical substances in these thick, dark brown or tan-colored tunics are unknown, these secondarily thickened bulb tunics are coded as a single state.

3. (10) *Leaf habit*: annual = 0, lasting longer than a year = 1.

A strictly annual growth pattern, in which just one set of foliage leaves is produced and shed each year, is found in most members of Amaryllideae and the outgroup. In contrast, *Crinum* species may either be evergreen or, as in *Ammocharis* and *Cybistetes,* they may have mature foliage leaves that die back during seasonal drought then regrow at the end of the dormant period. As Troll (1954) showed in *Ammocharis coranica* (Ker Gawl.) Herb., regrowth of the mature leaves is due to a well-developed intercalary meristem, which results in the truncate leaf apices that characterize most species in these genera. This growth pattern is particularly remarkable in plants of *Cybistetes longifolia* from the arid Richtersveld, southwestern Africa, in which the leaf blades elongate and die back up to three times during a single year in response to alternating wet and dry sequences (Snijman & Williamson, 1994).

4. (3) *Leaf number*: at least four = 0, two = 1.

A reduced number of foliage leaves is found in all species of *Hessea* and *Strumaria* subg. *Gemmaria.* Most individuals in these taxa have two leaves per year, but, rarely, three leaves have been recorded (Snijman, 1994). Four or usually more foliage leaves per shoot occur in all other Amaryllideae and in most genera of Haemantheae and the family.

5. **Leaf pigmentation*: unmarked = 0, speckled with red abaxially = 1.

Only in *Crossyne* are the leaves abaxially speckled with red, an autapomorphy for the genus.

6. **Leaf surface*: glabrous = 0, pubescent (at least in juveniles) = 1.

Leaves with soft, simple, uniseriate hairs (0.2–6.0 mm long) are unique to *Strumaria* subg. *Gemmaria*. Pubescence diminishes in some species of this group at maturity (*Strumaria* sect. *Bokkeveldia*) but is always present in juveniles. This specialization is treated as an autapomorphy.

7. (10) *Leaf margin*: unthickened = 0, heavily thickened = 1.

The leaf margins of *Brunsvigia* and *Crossyne* are raised with thick-walled cells, often giving the leaves a slightly crisped, reddened outline.

8. (10) *Leaf margin*: untoothed = 0, with thin-walled branching teeth = 1, with thick-walled branching bristles = 2.

Multiseriate, branching, cartilagenous cilia are present on leaf margins of *Crinum* (Arroyo & Cutler, 1984), *Ammocharis*, and *Cybistetes*, and these are thin-walled in comparison to the long, bristly cilia on the leaf margins of *Crossyne*. This multistate character is treated as unordered.

9. (4) *Pedicel length at anthesis*: equaling or less than perigone length = 0, at least twice the perigone length = 1.

Two variables determine inflorescence form at anthesis: pedicel length and flower size. A clustered inflorescence in which pedicel length is less than the perigone length predominates in Amaryllidaceae, but widely spreading inflorescences, with pedicels at least twice as long as the perigone, are characteristic of *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* subg. *Tedingea*. The states slightly overlap in *Nerine* and *Carpolyza*, but when partitioned according to the method of Almeida and Bisby (1984), the data for these taxa could be reliably scored (Snijman, 1992).

10. (10) *Flower color during senescence*: pigmentation accentuated = 0, pigmentation lost = 1.

Verdoorn (1973) first drew attention to color changes in the flowers of Amaryllideae when she noted that floral pigmentation in most southern African *Crinum* species is accentuated with age, whereas in a few species it is lost. Enhanced coloring is common in the senescent flowers of all genera of Amaryllideae and Haemantheae, except in *Hessea*, where pigmentation is consistently lost in all species. *Crossyne*, whose two species have contrasting states, was treated as indeterminate, and *Crinum* was scored as plesiomorphic until additional data clarify the interpretation.

11. (2) *Stamen position*: spreading = 0, declinate = 1.

Declinate stamens, absent from the outgroup, are consistently found in *Amaryllis*, *Nerine*, and *Brunsvigia*. Both states occur in *Crinum* and *Crossyne*, which are treated as indeterminate.

12. (4) *Staminal tube*: absent = 0, rudimentary = 1, conspicuous = 2.

Stamens in Amaryllideae are either separate (*Ammocharis*, *Boophone*, *Crinum*, and *Cybistetes*) or proximally connate to varying degrees. The connation in *Amaryllis*, coded as rudimentary, is extremely short (ca. 1 mm) and extends above the confluence of only the outer tepal whorl before becoming free. In *Nerine*, *Brunsvigia*, *Crossyne*, and *Hessea*, the staminal tube extends shortly to well above the confluence of both inner and outer tepal whorls, and is thus coded as conspicuous. Representatives of *Hessea* subg. *Hessea* may have the longest staminal tubes in the tribe, up to 4 mm long, in contrast to those of *Hessea* subg. *Namaquanula*, in which the tube is almost absent, putatively a secondary reduction (Snijman, 1994).

The interpretation of the stamens in *Strumaria* subg. *Strumaria* is more complex. Although separate in *S. bidentata* Schinz, the stamens in the remaining four taxa are connate. Serial sections in *S. truncata*, however, indicate that the outer stamens are proximally adnate to the style (Snijman, 1994). Thus the staminal connation in *Strumaria* subg. *Strumaria* is regarded as autapomorphic and treated independently from the staminal tube in other genera of Amaryllideae.

13. **Filament trichomes*: trichomes absent = 0, trichomes present = 1.

The filaments are smooth in all Amaryllideae and Haemantheae, except *Hessea* subg. *Namaquanula*, where they are proximally covered with short trichomes on the adaxial surface (Snijman, 1994).

14. **Filament morphology*: both whorls uniform = 0, outer and inner whorls dimorphic =1.

Unknown elsewhere in Amaryllidaceae are the specialized, dimorphic filaments of *Hessea stenosiphon* (Snijman) D. & U. Müll.-Doblies. The short outer filaments occlude the perigone throat, whereas the inner filaments of this species are erect and club-shaped, with a structural composition highly representative of osmophores as described by Vogel (1990). The epidermal cells are densely cytoplasmic and the inner parenchyma contains strikingly conspicuous masses of starch (Snijman, 1994). Fra-

grance emission from these structures is still to be tested.

15. (4) *Anther attachment*: ± dorsifixed = 0, in a short connective sheath (subcentrifixed) = 1, in a long connective sheath (centrifixed) = 2.

Previously described as "basifixed" (Baker, 1888, 1896; Dyer, 1976; Phillips, 1951; Traub, 1963), the anthers of *Hessea* and *Carpolyza* were recently redefined in terms of the degree to which the filament tip is inserted into a tube formed by the anther connective. The relative lengths of the dorsal and ventral walls of the tubular connective enabled D. and U. Müller-Doblies (1985) to recognize three states of anther attachment: dorsifixed anthers (relative lengths less than 50%), subcentrifixed anthers (relative lengths 50–75%), and centrifixed anthers (relative lengths more than 75%). Despite their apparent arbitrary subdivision, current data indicate that the states are only slightly overlapping. Anthers are dorsifixed in the outgroup and in most genera of Amaryllideae; subcentrifixed in *Hessea* subg. *Namaquanula*, *Strumaria* subg. *Gemmaria*, and *Carpolyza*; and centrifixed in *Hessea* subg. *Hessea*. The interpretation of the anther attachment in *Hessea* subg. *Kamiesbergia* is not yet resolved (Müller-Doblies, 1992; Snijman, 1994). To reflect the hypothesized morphocline in anther attachment, the character states are treated as additive.

16. (10) *Pollen morphology* : monosulcate = 0, bisulculate = 1.

Relative to the large, boat-shaped-elliptic, monosulcate pollen grains in other genera of Amaryllidaceae (Meerow, 1995), pollen grains of Amaryllideae are consistently bisulculate and normally dispersed at the two-celled stage (Dutt, 1962; Erdtman, 1966; Howell & Prakash, 1990; Schulze, 1984).

17. (10) *Pollen exine*: reticulate = 0, spinulose = 1.

Unlike reticulate exine elsewhere in Amaryllidaceae, surface ornamentation of pollen is uniform in Amaryllideae; gemmate with scattered large spinulae (Meerow, 1995).

18. (1) *Style position*: symmetrically placed = 0, laterally displaced = 1.

The style is uniformly symmetrically placed in the outgroup, *Boophone*, *Ammocharis*, *Hessea*, *Strumaria*, and *Carpolyza*. All remaining Amaryllideae have a laterally displaced style. Lateral displacement of the style is usually associated with declinate stamens but in certain species of *Crinum*, *Crossyne*, and *Cybistetes* the stamens remain evenly spread.

19. (10) *Style form*: slender = 0, proximally enlarged = 1.

With the exception of *Strumaria*, the style in Amaryllideae and the outgroup is typically slender. Goldblatt (1976) first recognized the proximally enlarged style in *Strumaria* as a derived, unique character. The stylar swellings are variable but take three basic forms: increasingly thickened upward then abruptly narrowed above (*Strumaria* subg. *Tedingea*); more or less equally thickened in the lower half (subg. *Strumaria*); or distinctly broadest at the base and gradually tapering upward (subg. *Gemmaria*) (Snijman, 1994).

20. (10) *Nectar collection site*: pooled around the style base = 0, in three discrete sites in the axils between the inner filaments and style = 1.

Nectar collects in a central well around the base of the style in the outgroup and in most genera of Amaryllideae. This contrasts with *Carpolyza* and *Strumaria*, where nectar collects in three discrete sites, in the axils between the inner filaments and the style base. These separate nectar collection sites vary in depth and diameter. In most species (*Carpolyza*, *Strumaria* subg. *Tedingea* and subg. *Gemmaria*), the site is shallow, holding nectar in a single large droplet. Through lengthwise and radial extension of the confluence formed by the outer filament whorl and style in *Strumaria* subg. *Strumaria*, the volume of the cavities between the inner filaments and style has been increased, and deep nectar wells have developed. Preliminary studies have shown that within *Strumaria*, nectary anatomy is quite diverse. Without exception the nectaries are septal, but considerable variation is found in the position of the nectaries relative to the locules, in their size, and their degree of convolution. Although the extent of septal nectary diversity in Amaryllideae does not approach that reported in Haemodoraceae (Simpson, 1993), a detailed study of floral anatomy may give further insight into the tribe's functional floral morphology.

21. (10) *Ovule*: bitegmic = 0, unitegmic = 1.

In contrast to the bitegmic ovules of most Amaryllidaceae, the ovules in Amaryllideae are unitegmic. Representatives reported to have a solitary integument are *Amaryllis* (Markötter, 1936; Oganezova, 1990; Schlimbach, 1924); *Boophone disticha* (Schlimbach, 1924); *Brunsvigia minor* Lindl. and several *Crinum* species (Hofmeister, 1861); *Cybistetes* (Markötter, 1936); and *Nerine sar-*

niensis (L.) Herb. (= *N. curvifolia* Herb.) (Goebel, 1932).

Furthermore, several species of *Crinum* have been described as having ategmic ovules (Toilliez-Genoud, 1965; Tomita, 1931). However, the definitive embryological studies of Dutt (1957a, b, 1959, 1962) and Venkateswarlu and Lakshmi (1978), on a range of *Crinum* species, present strong evidence for the existence of an integument before its loss during the transformation of the ovule into the seed. The present study also confirms the presence of unitegmic ovules in *Brunsvigia* and *Nerine* (see Appendix I) and reports their presence in *Crossyne*, *Hessea*, and *Strumaria*. This current data give further support to Huber's (1969) hypothesis that unitegmic ovules are synapomorphic for the tribe.

22. (1) *Scape habit during seed dispersal*: withering back after seed release = 0, detaching at ground level after seed release from the capsules = 1, detaching at ground level before seed release from the capsule = 2. 23. **Habit of fruiting cluster during seed dispersal*: remaining attached to scape = 0, detaching from scape = 1.

At maturity the scape in Amaryllideae varies in its duration and place of abscission. The scape persists above ground until long after seed release, then slowly withers away in the outgroup, *Amaryllis*, *Ammocharis*, *Boophone*, *Crinum*, and *Strumaria* subg. *Strumaria*. Elsewhere in the tribe, the scape detaches from the bulb at ground level soon after seed release (*Carpolyza*, *Nerine*, and *Strumaria* subg. *Tedingea*) or before the release of seed from the capsules (*Cybistetes*, *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* subg. *Gemmaria*). Thus through early abscission of the scape in the latter five taxa, the entire infructescence becomes the main unit of dispersal. Dispersal is similar in *Boophone*, but the structural unit is uniquely derived by the abscission of the entire fruiting cluster from the top of the scape. Multistate character 22 is treated as ordered, and until the abscission tissues of the scape are studied anatomically, the states are considered to be homologous.

24. (10) *Fruit*: dehiscent = 0, indehiscent = 1.

In the outgroup indehiscent fruits occur in four genera, whereas a dehiscent capsule is found only in *Cyrtanthus* L.f. Dehiscent capsules also occur uniformly in the closely similar Hippeastreae and Lycorideae (Dahlgren et al., 1985) and in Alliaceae, which molecular data identified as basal to Amaryllidaceae (Fay et al., 1994). Although not common in the outgroup, the existence of dehiscent capsules in one representative, as well as at a level immediately basal to the Amaryllidaceae, formed the basis for selecting capsule dehiscence as the outgroup character state. This coding parallels Dahlgren and Rasmussen's (1983) hypothesis that baccate fruits are secondarily derived from capsules in Amaryllidaceae.

25. (10) *Developing fruit*: never rostellate = 0, rostellate = 1.

Ammocharis, *Boophone*, *Crinum*, and *Cybistetes* have fruits which, while developing, are beaked with the persistent base of the perigone tube. The beak persists on the mature fruits only in *Crinum*, and its final length has proved to be diagnostically valuable in many species (Nordal & Wahlstrøm, 1980; Verdoorn, 1973). None of the other members of Amaryllideae or the outgroup has beaked fruits.

26. (10) *Mature fruit*: ± regular = 0, irregular = 1. 27. **Mature fruit*: not large = 0, conspicuously enlarged = 1.

The form of the fruit is more or less symmetrical in Amaryllideae except in *Ammocharis*, *Crinum*, and *Cybistetes*, where it is molded by the enclosed developing seeds. As the shape of the seeds is often extremely variable (Manasse, 1990; Snijman & Williamson, 1994; Toilliez-Genoud, 1965), the fruit also assumes an irregular form. Conspicuously large, obconical to rarely spindle-shaped capsules (reaching up to 60 mm long and 25 mm across in many species), with visible transverse veining, are autapomorphic for *Brunsvigia*.

28. (10) *Testa*: without stomata = 0, stomatose = 1.

Although not common in the outgroup Haemantheae, dry seeds, crusted with phytomelan, occur in one representative, *Cyrtanthus*; widely in other Amaryllidaceae; and consistently in Alliaceae, the family basal to Amaryllidaceae (Fay et al., 1994). In contrast, the mature seeds of Amaryllideae are water-rich and lack phytomelan in the coat. Schlimbach (1924) was the first to report stomata on the seed coat of *Nerine sarniensis* (= *N. curvifolia*), and Boyd (1932) later recorded them in *Carpolyza spiralis* (L'Hérit.) Salisb. A survey of the testa in this study has shown that stomata are also present on the seeds of additional representatives of *Nerine*, in *Brunsvigia*, *Crossyne*, *Hessea*, and *Strumaria* (Appendix I). The stomata are anomocytic (Fig. 5B–E), as is typical for Amaryllidaceae (Arroyo & Cutler, 1984; Dahlgren & Clifford, 1982), and the surrounding cells are covered by a sculptured cuticle (Fig. 5D, E), in which the central striations become increasingly thick and sinuous with age.

29. (10) *Integument in developing seed*: disintegrating = 0, enlarging = 1. 30. (10) *Integument in developing and mature seed*: without chlorophyll = 0, chlorophyllous = 1.

In *Brunsvigia, Crossyne, Nerine, Hessea, Strumaria,* and *Carpolyza* the integument expands into a water-rich, chlorophyllous tissue with vascular strands. As reported in *N. sarniensis* (= *N. curvifolia*) this is achieved by increasing the number and the size of the cells after fertilization (Schlimbach, 1924), and when finally ripe, the integument contains rich amounts of starch and chlorophyll (Goebel, 1932) (Fig. 4B–D). In the other representatives of Amaryllideae the integument remains undifferentiated and finally disintegrates (Dutt, 1970; Venkateswarlu & Lakshmi, 1978), whereas in the outgroup, the integuments of seeds shed in a dry, dormant state are crushed at maturity.

31. (10) *Endosperm in mature seed*: undifferentiated externally = 0, formed into cork externally = 1. 32. (10) *Mature seed*: without chlorophyll in endosperm = 0, endosperm with chlorophyll = 1.

A novel feature in *Ammocharis, Boophone, Crinum,* and *Cybistetes* is the development of a few layers of cork tissue from the peripheral cells of the endosperm (Fig. 4E, F). Although well known in *Crinum* (Merry, 1937; Schlimbach, 1924; Venkateswarlu & Lakshmi, 1978) and *Cybistetes* (= *Ammocharis falcata* sensu Markötter, 1936), a cork-covered endosperm is reported here in two additional genera: *Boophone* and *Ammocharis* (Fig. 5F, H). Another novel feature in these genera is that chloroplasts occur in the peripheral cell layers beneath the phellogen, even when the seed is covered by the pericarp (Dutt, 1957a, 1962; Schlimbach, 1924). *Amaryllis* is the only taxon of Amaryllideae in which the extensively developed endosperm does not have corky or chlorophyllous outer layers (Schlimbach, 1924) (Fig. 4A). In all other Amaryllideae the endosperm remains undifferentiated and comparatively poorly developed.

33. (10) *Embryo*: without green pigment = 0, green = 1.

Dahlgren and Clifford (1982) suggested that the embryo of *Crinum* could be chlorophyllous. Since then Howell and Prakash (1990) recorded this feature in *Crinum flaccidum* Herbert, while our study confirms the presence of green-pigmented embryos in every genus in Amaryllideae. The chlorophyll content, however, is yet to be investigated.

34. (10) *Basic chromosome number*: 11 = 0, 10 = 1.

Chromosome numbers in Amaryllideae are well known (Goldblatt, 1972; Gouws, 1949; Nordal & Wahlstrøm, 1980) and a karyotype of $x = 11$ is considered basic in Amaryllideae (Goldblatt, 1976) and the family (Inariyama, 1937; Meerow, 1984; Satô, 1938). Species of *Carpolyza* and *Strumaria* have a reduced base number of $x = 10$ (Goldblatt, 1976; Snijman, 1994), the only exception being *S. pygmaea* Snijman, which has $x = 11$. Although most taxa in Haemantheae have $x = 9$ and 8 (Inariyama, 1937; Ising, 1970; Vosa & Marchi, 1980) some species of *Clivia* have the base number of $x = 11$ (Gouws, 1949).

OUTGROUP SELECTION

Traub's (1962, 1963) tribal classification of Amaryllidaceae provides a valuable framework for selecting an outgroup that has synapomorphies shared with the ingroup (see Nixon & Carpenter, 1993). Traub's system divides the currently recognized tribes (Dahlgren et al., 1985) into two infrafamily groups, the Amarylloidinae and the Pancratioidinae. Within the Amarylloidinae, the apparent close similarity between representatives of Amaryllideae and Hippeastreae (Brummit, 1987) is based essentially on highly homoplasious floral characters, but the pollen, fruit, and seed characters are discontinuous (see Meerow, 1995). Other differences between the two tribes are root and scape structure, and spathe valve arrangement, and in these characters Haemantheae is intermediate (Arroyo & Cutler, 1984). The close relationship postulated to exist between Haemantheae and Amaryllideae, for which equitant spathe valves (Arroyo, 1984) is a possible synapomorphy, thus accounts for our choice of Haemantheae as outgroup to root the cladogram. All the characters defined for the analysis of the Amaryllideae apply also to the outgroup Haemantheae.

DELIMITATION OF GENERA IN AMARYLLIDEAE

All the currently recognized genera of Amaryllideae were examined to ensure that their delimitation could reasonably be considered monophyletic. This is accomplished by identifying hypothetical synapomorphies of the ingroups relative to other taxa (Nixon & Carpenter, 1993). *Amaryllis, Carpolyza,* and *Cybistetes* were accepted as monophyletic by virtue of their being monotypic.

Boophone sensu lato (five species) has commonly been distinguished from other genera of Amaryllideae by large bulbs, inflorescences of more than 100 flowers, a perigone with tube shorter than the tepals, long pedicels in fruit, and triquetrous dry

fruits with solitary or few seeds per locule (Dyer, 1976; Nordal, 1982). Milne-Redhead and Schweickerdt (1939) first questioned the inclusion of species with both dehiscent and indehiscent fruits in *Boophone* and recommended that the generic limits be reexamined. In agreement with Müller-Doblies (1994), three groupings have been proposed for the five species.

(1) *Boophone disticha* and *Boophone haemanthoides* F. M. Leight. share indehiscent, beaked fruits, which are also found in *Crinum*, *Ammocharis*, and *Cybistetes*. However, the species are uniquely characterized by the abscission of the fruiting head from the top of the scape. Consequently, this species pair, which includes the type species of *Boophone*, is considered to be monophyletic. (2) *Boophone guttata* (L.) Herb. and *Boophone flava* W. F. Barker ex Snijman have leaves abaxially speckled with red, and fringed with long, rigid, branching hairs. These two unique features are taken as evidence of the monophyly of the species pair, and they are assigned to the genus *Crossyne*, which was recently resurrected by D. and U. Müller-Doblies (1994). (3) *Boophone pulchra* W. F. Barker shares none of the putative synapomorphies recognized for the newly defined *Boophone* and *Crossyne*. Possible derived characters in *Boophone pulchra*, relative to the tribe as a whole, include the presence of macropapillae on the adaxial leaf epidermis and enlarged, usually triquetrous capsules, features that occur in species of *Brunsvigia*. For the phylogenetic analysis of Amaryllideae, *Boophone pulchra* is, therefore, treated as belonging to *Brunsvigia* in accordance with D. and U. Müller-Doblies (1994). The only feature in which *Brunsvigia pulchra* (W. F. Barker) D. & U. Müll.-Doblies differs from other *Brunsvigia* species is the elongation of the pedicels after anthesis rather than prior to anthesis. Although typical of *Boophone* sensu stricto, this character state occurs in several other members of the tribe (*Amaryllis* and *Cybistetes*) and cannot be recognized as autapomorphic for *Boophone* sensu stricto.

Crinum is currently regarded as the largest genus in the tribe with ca. 65 species (Fangan & Nordal, 1993). Species concepts of these ornamental plants have traditionally been too narrow (Fangan & Nordal, 1993; Hannibal, 1985), and thus far revisional work for the African floras has resulted in a reduced number of taxa being upheld (Nordal, 1977). The genus is cytologically variable (Nordal & Wahlstrøm, 1980), but vegetative and floral diversity is comparable to that of other genera of Amaryllideae (*Brunsvigia*, *Hessea*, and *Strumaria*). Flowers vary from hypocrateriform to funnel-shaped or bell-shaped, with spreading or declinate stamens; the leaves, which sometimes form a false-stem, are channeled or ribbed, thin-textured or fleshy, with intact or truncate tips (Nordal, 1977). The truncate leaf apices, which also occur in *Ammocharis* and *Cybistetes*, result from a well-developed and putatively derived intercalary meristem (Troll, 1954), which enables the leaves to die back and regrow over several seasons. Evident synapomorphies do not exist to separate *Crinum* from *Ammocharis*; therefore, *Crinum* is probably paraphyletic with *Ammocharis* and *Cybistetes* embedded in it. However, for the analysis *Ammocharis* and *Cybistetes* are provisionally retained, as suggested by Snijman and Williamson (1994), and following the recommendations of Nordal (1977) and Verdoorn (1973) existing subgeneric divisions of *Crinum* are avoided because they are so weakly supported.

Nerine, with ca. 23 species, is possibly the second largest genus of Amaryllideae. Genera of Amaryllideae are distinguished by subtle floral characters, and the extremely similar floral morphology shared by species of *Nerine* provides good evidence for the proposed monophyly of the genus. The characteristic attenuate, more or less crisped, tepal outline of *Nerine* species is a likely synapomorphy for the genus.

Brunsvigia (19 species) is uniquely macropapillate on the adaxial leaf epidermis in many species (Arroyo & Cutler, 1984), and large, inflated capsules (sometimes up to 70 mm long) with visible transversal veins occur in all the species. Both features provide good evidence for the inclusion of *Boophone pulchra* in *Brunsvigia*. Although not inflated, similarly shaped, somewhat triquetrous or elongated dry fruits also exist in *Boophone* sensu stricto and *Cybistetes*. The different mode of dehiscence in the latter genera (indehiscent as opposed to dehiscent: character 24) suggests, however, that the fruits have been separately derived. The enlarged capsule is regarded here as evidence for the monophyly of *Brunsvigia*.

Hessea (13 species) and *Strumaria* (23 species), commonly distinguished by their consistently actinomorphic flowers, are the only genera of Amaryllideae currently classified to reflect explicitly established phylogenetic relationships. *Hessea*, with three subgenera, is defined by one unique synapomorphy: the total loss of floral pigmentation at senescence (Snijman, 1994). The synapomorphy for *Strumaria*, also with three subgenera, is the uniquely swollen or winged style base (Snijman, 1994). In order to provide maximum structure for the phylogeny of Amaryllideae, the reliably monophyletic subgenera of *Hessea* and *Strumaria* were

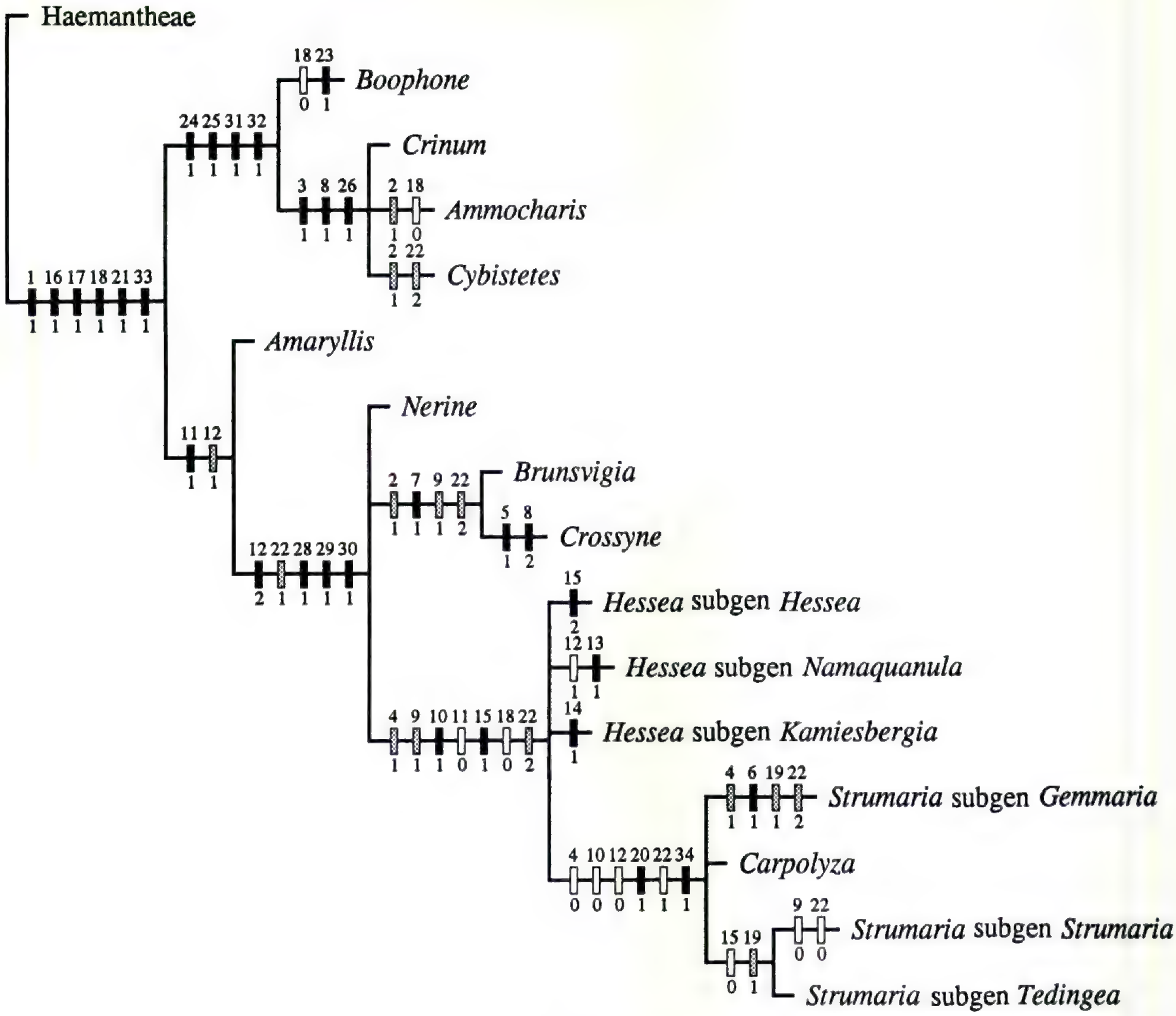

Figure 1. Strict consensus tree of Amaryllideae. Solid bars indicate non-homoplasious synapomorphies; gray bars indicate parallelisms and open bars indicate reversals.

also included in the analyses. All taxa included in the phylogenetic analyses are listed in Table 2.

Results

The cladistic analyses with equal character weighting (excluding autapomorphies) gave 16 minimal length cladograms of 54 steps, a consistency index (CI) of 0.68, and a retention index (RI) of 0.80. The strict consensus tree (Fig. 1) generated by PAUP and Hennig86 shows that all 16 cladograms agree in the following respects. (1) *Boophone, Crinum, Ammocharis,* and *Cybistetes* appear as a monophyletic group. (2) *Amaryllis* resolves as basal to *Nerine, Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria.* (3) *Brunsvigia* and *Crossyne* resolve in a monophyletic clade. (4) *Hessea, Carpolyza,* and *Strumaria* form a monophyletic group.

Successive weighting retrieved 2 of the 16 most parsimonious trees. These differ only in the degree of resolution shown in the *Hessea* clade. The tree that we have chosen for interpreting character evolution (Fig. 2) differs from the strict consensus tree (Fig. 1) as follows. (1) The *Crinum–Ammocharis–Cybistetes* clade is more fully resolved. (2) *Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria* form a clade that resolved in 14 of the 16 minimal length trees. (3) A clade of *Hessea* subgenera, which was retrieved in 10 of the 16 minimal length trees, is present. (4) The subgenera of *Strumaria* are present in a clade. Support for this component is more complex. *Strumaria* subg. *Gemmaria* is basal to *Carpolyza* and *Strumaria* subg. *Tedingea* and subgenus *Strumaria* in 10 of the minimal length trees, but this component is supported only by the homoplasious character 22(1) (CI 0.28, RI 0.54). In contrast, *Carpolyza* resolves as basal to the clade of *Strumaria* subgenera in 6 of the trees retrieved. However, character 19 (style proximally enlarged, CI 1.00 and RI 1.00), which supports the *Strumaria* clade, is unique in Amaryllidaceae (Snijman,

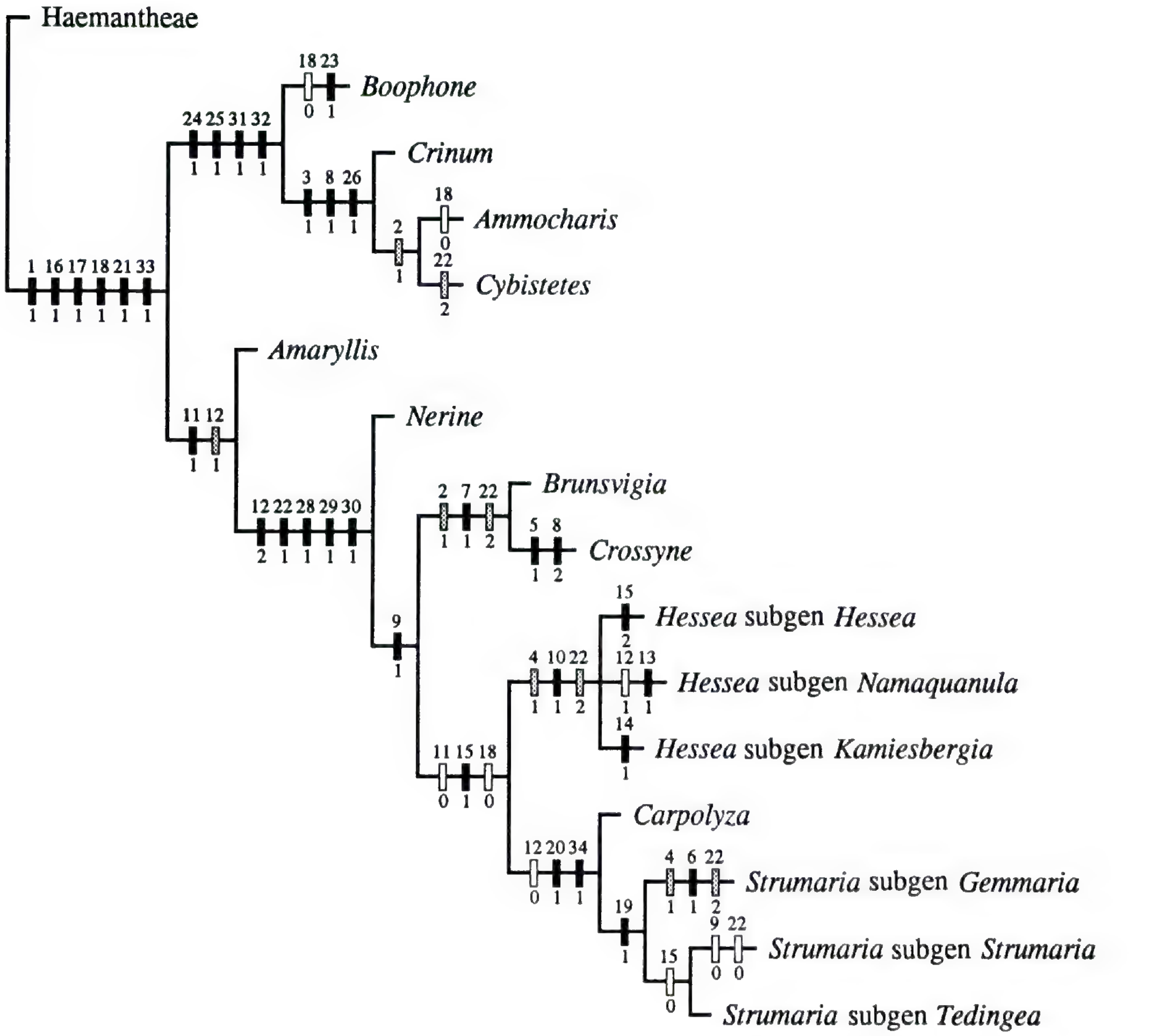

Figure 2. The preferred most parsimonious cladogram of Amaryllideae. Solid bars indicate non-homoplasious synapomorphies; gray bars indicate parallelisms and open bars indicate reversals.

1994), and we therefore accept the topology of the *Carpolyza–Strumaria* component in our preferred tree with confidence (Fig. 2). Lastly, the differences in resolution obtained in the *Crinum–Ammocharis–Cybistetes* clade in the strict consensus tree (Fig. 1) and the preferred most parsimonious tree (Fig. 2) do not alter our discussion of seed character and dispersal system evolution.

When *Amaryllis* was placed at the base of the *Boophone–Crinum–Ammocharis–Cybistetes* clade, as suggested by the classifications of Traub (1957, 1962, 1963), the topology was 2 steps longer than our most parsimonious tree. The placement of *Amaryllis* in a position basal to the two major clades gave a topology 1 step longer than the minimal length cladogram. When parsimony was relaxed by 2 steps, 1404 trees were generated and resolution was lost in all branches except the *Crinum–Ammocharis–Cybistetes* clade and the *Brunsvigia–Crossyne* clade.

Discussion

Relationships within Amaryllideae

All previous classifications of Amaryllideae (Table 1) placed the *Boophone–Cybistetes* clade, *Amaryllis*, *Nerine*, and *Brunsvigia* in Amaryllidinae. Our cladistic analysis clearly shows that subtribe Amaryllidinae (=Crininae sensu Traub, 1957, 1963) is paraphyletic with *Crossyne* and Strumariinae (the *Hessea–Carpolyza–Strumaria* clade) embedded in it. Strumariinae, the only other subtribe previously recognized (Müller-Doblies, 1985), is monophyletic.

In order to recognize the monophyletic groups generated by the cladistic analysis we propose a new classification. It is widely accepted that nomenclature is most effective if taxon names are stable. Thus prior to translating cladistic results into new classifications, Linder (1991) recommends an assessment of the nodes that are unlikely to change

with the addition of new data. Since *Amaryllis* is the oldest valid name available for typification at subtribal level, the stability of its position is of particular importance. Our results best support the placement of *Amaryllis* basal to *Nerine, Brunsvigia, Crossyne, Hessea, Carpolyza,* and *Strumaria.* We have therefore chosen to join the Strumariinae clade with *Crossyne, Brunsvigia, Nerine,* and *Amaryllis* to form a more inclusive clade, which is formally named subtribe Amaryllidinae. The *Boophone, Crinum, Ammocharis,* and *Cybistetes* clade is accordingly recognized as a second subtribe: the emended Crininae. The option of recognizing a third subtribe, containing only *Amaryllis,* was also considered but we regard the formal classification given below to be more conservative in reflecting the presently understood relationship of *Amaryllis* to *Nerine* and other representatives of its clade. Nomenclatural stability within Amaryllideae is thus maintained until strong support to the contrary becomes available.

REVISED CLASSIFICATION OF THE TRIBE AMARYLLIDEAE

Tribe **Amaryllideae**

Bulb scales when torn produce extensible cottony threads; flowers actinomorphic or zygomorphic; pollen bisulculate; ovule unitegmic; seed water-rich with green embryo. Includes about 55 species. Mostly African but with several *Crinum* species in the tropics of Asia, Australia, and America, Madagascar, and the Mascarene and Pacific Islands.

Subtribe **Amaryllidinae** Pax in Engler & Prantl, Nat. Pflanzenfam. 2, 5: 105. 1887.

Scape usually abscissing at ground level; stamens declinate (except in *Hessea, Strumaria,* and *Carpolyza*), connate into a tube proximally (except in *Strumaria* and *Carpolyza)*; seed (except in *Amaryllis*) with a well-developed chlorophyllous integument and stomatose testa. Includes 82 known species.

Amaryllis Linnaeus, Sp. Pl.: 292. 1753.

Flowers zygomorphic; stamens connate proximally into a rudimentary filament tube; seeds colorless or pink. Monotypic.

Nerine Herbert in Bot. Mag. 47: t. 2124. 1820.

Flowers zygomorphic; tepals attenuate, margins ± crisped. 23 species (Traub, 1967).

Brunsvigia Heister, Beschr. neu. Geschl.: 3. 1755.

Bulb scales usually thick and brittle; leaf margins raised; flowers zygomorphic; capsule enlarged, turbinate or fusiform with visible transverse veins; scape detaching at ground level; infructescence dispersed as a single unit. 19 species (Dyer, 1950, 1951).

Crossyne Salisbury, Gen. Pl.: 116. 1866.

Bulb scales thick and brittle; leaves speckled with red abaxially, margins raised and fringed with long, stiff trichomes; inflorescence 100- or more-flowered; flowers zygomorphic, sometimes only weakly so by deflexed style; scape detaching at ground level; infructescence dispersed as a single unit. 2 species (Müller-Doblies, 1994).

Hessea Herbert, Amaryllidaceae: 289. 1837.

Leaves usually 2; flowers actinomorphic, aging to brown; filaments inserted into a sheath formed by anther connective (centrifixed to subcentrifixed), except in *H. bruce-bayeri* (D. & U. Müll.-Doblies) Snijman and *H. stenosiphon* (Snijman) D. & U. Müll.-Doblies; infructescence dispersed as a single unit. 13 species (Snijman, 1994).

Strumaria Jacquin, Collectanea 5: 49. "1796" [1797].

Leaves up to 6, then usually arranged in a fan (subg. *Strumaria*), or mostly 2 and pubescent, at least in juveniles (subg. *Gemmaria*); flowers actinomorphic; filaments of outer or both whorls proximally adnate to style, usually inserted into a sheath formed by anther connective (subcentrifixed); style proximally swollen or winged; nectar collects in axils between inner filaments and style; basic chromosome number $x = 10$ (except in *S. pygmaea* Snijman, where $x = 11$). 23 species (Snijman, 1994).

Carpolyza Salisbury, Parad. Lond. 1: t. 63. 1807.

Flowers actinomorphic; inner filaments adnate to style proximally, inserted into a sheath formed by anther connective (subcentrifixed); nectar collects in axils between inner filaments and style; basic chromosome number $x = 10$. Monotypic (Snijman, 1994).

Subtribe **Crininae** Pax in Engler & Prantl, Nat. Pflanzenfam. 2, 5: 108. 1887.

Flowers actinomorphic or zygomorphic; fruit indehiscent, rostellate at least during development; seeds lacking an integument, endosperm-rich, cork-covered, with several layers of chlorophyll-containing cells below the phellogen. Includes ca. 73 species.

Table 3. Distributions and favored habitats of genera of Amaryllideae. Number of species is given in parentheses. Southern Africa is defined as the area south of a line between the Kunene and Zambezi rivers.

	Distribution	Habitat
Subtribe CRININAE		
Boophone (2)	Tropical East Africa to southern Africa	Open plains or slopes
Crinum (ca. 65)	Tropics of Africa, Asia, Australia & America, southern Africa, Madagascar, Mascarene & Pacific Islands	Moist sites, forests, river edges, seasonal pools or salt pans
Ammocharis (5)	Tropical East Africa to southern Africa	In rocks or seasonally wet places
Cybistetes (1)	Winter-rainfall region of southern Africa	Open sites
Subtribe AMARYLLIDINAE		
Amaryllis (1)	Winter-rainfall region of South Africa	Mesic places
Nerine (23)	Southern Africa	Mesic places
Brunsvigia (19)	Southern Africa	Open plains or rocky sites
Crossyne (2)	Winter-rainfall region of South Africa	Open places
Hessea (13)	Winter-rainfall region of southern Africa	In rocks and seasonally moist sites
Strumaria (23)	Winter-rainfall region of southern Africa	In rocks and seasonally moist sites
Carpolyza (1)	Winter-rainfall region of South Africa	In rocks and seasonally moist places

Crinum Linnaeus, Sp. Pl.: 291. 1753.

Leaves perennial, often formed into a false-stem, fringed with cartilaginous teeth, apex often truncate; flowers zygomorphic, sometimes only weakly so; fruit irregular, wall membranous to spongy. The genus has not yet been revised over its entire distribution range, but good regional treatments are available for Africa (Nordal, 1977, 1982; Nordal & Wahlstrøm, 1980; Verdoorn, 1973). Includes ca. 65 species (Fangan & Nordal, 1993) with ca. 40 in Africa. The genus is probably paraphyletic.

Ammocharis Herbert, Appendix: 17. 1821.

Leaves perennial; somewhat falcate, fringed with cartilaginous teeth, apex often truncate; flowers actinomorphic; fruit with membranous walls, irregular. 5 species (Milne-Redhead & Schweickerdt, 1939).

Cybistetes Milne-Redhead & Schweickerdt in J. Linn. Soc., Bot. 52: 191. 1939.

Leaves perennial, fringed with cartilaginous teeth, apex of mature leaves truncate; flowers weakly zygomorphic; scape detaching at ground level; infructescence dispersed as a single unit. Monotypic. The genus is probably nested in *Ammocharis* (Snijman & Williamson, 1994).

Boophone Herbert, Appendix: 18. 1821.

Leaves erect, distichous; flowers actinomorphic; fruiting head detaching from top of scape, dispersing as a single unit. 2 species.

PHYTOGEOGRAPHY AND PHENOLOGY

A comparison of the present distribution patterns of subtribes Amaryllidinae and Crininae (Table 3) shows that Crininae is widespread in the tropical and temperate regions of sub-Saharan Africa (Fig. 3). One genus, *Crinum,* is pantropical, with ca. 40 of its ca. 65 species in Africa (Nordal, 1982). Approximately 20 *Crinum* species occur in southern Africa, but only one is known from the winter-rainfall region (Verdoorn, 1973). Only three other representatives of Crininae (*Boophone disticha, Boophone haemanthoides,* and *Cybistetes*) are known in the temperate winter-rainfall region of southern Africa, although one of these (*Boophone disticha*) also ranges widely into central Africa. In contrast, Amaryllidinae is confined to the temperate regions of southern Africa (Fig. 3). Most *Nerine* species are known from the summer-rainfall region. *Brunsvigia* ranges widely over both summer- and winter-rainfall regions, whereas all the remaining representatives (*Amaryllis, Crossyne, Hessea, Carpolyza,* and all but two *Strumaria* species) are restricted to the winter-rainfall region of southern Africa. Most representatives of Crininae flower and fruit in summer during the leafing period. This differs in Amaryllidinae, where some species are summer-flowering but most flower and fruit in autumn, after the vegetative phase of the previous winter, which offers a short growing period.

SEED CHARACTERS IN AMARYLLIDEAE

Throughout the tribe, the seeds are water-rich, nondormant, and have chlorophyllous embryos. As

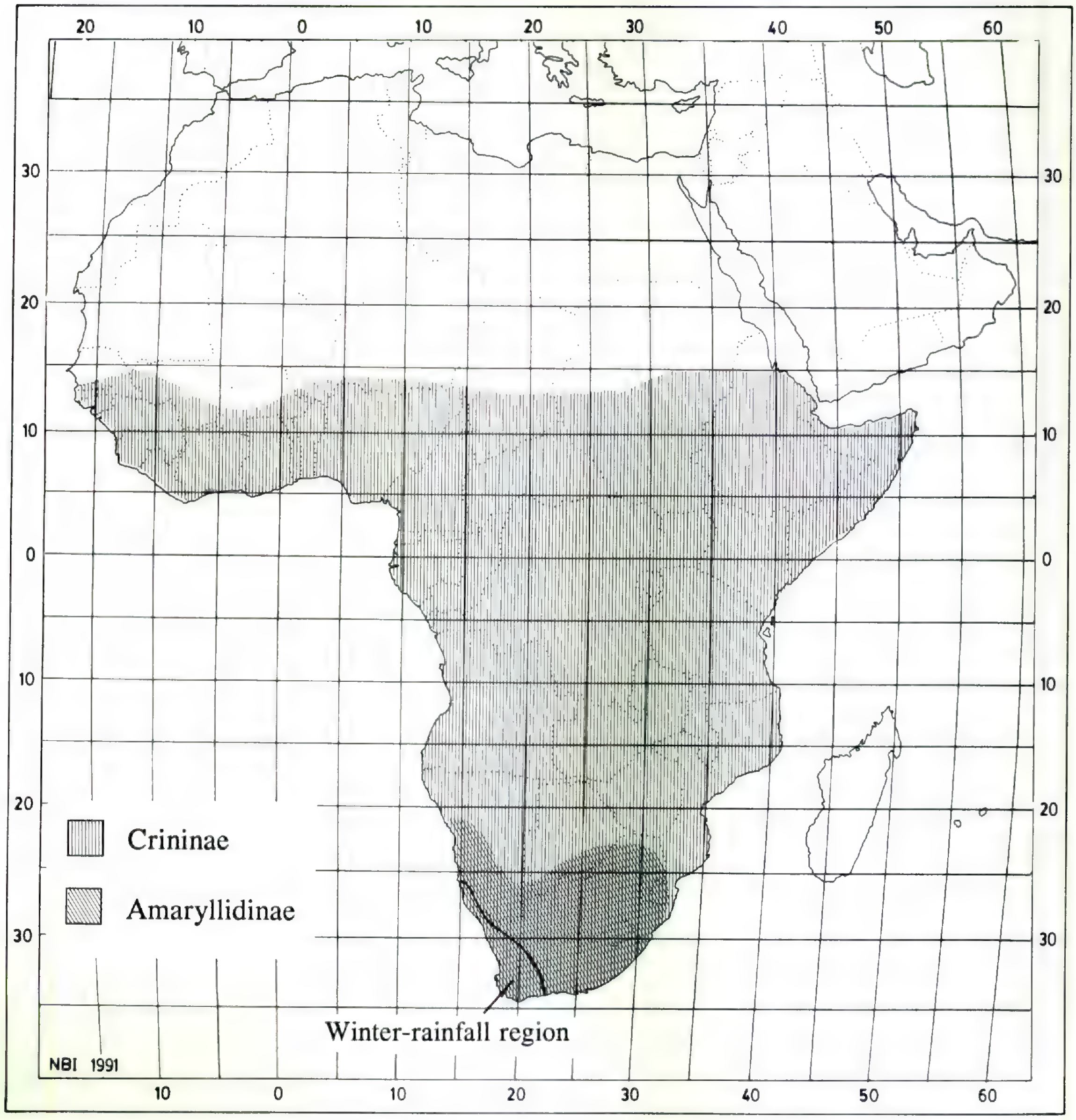

Figure 3. Distributions of subtribes Amaryllidinae and Crininae in Africa.

commented on by several authors (see Rendle, 1901), the seeds are large (at most 20–30 mm across in *Crinum*) but not necessarily heavy (Boyd, 1932; Dutt, 1962), and they germinate easily without additional water (Beaurieux, 1914; Howell & Prakash, 1990; Isaac & McGillivray, 1965). In comparison to other Amaryllidaceae, the embryos of Amaryllideae seeds have a cotyledon with a particularly well-developed vascular system that contributes to seedling vigor, as reported by Boyd (1932). This can be seen in the rapid elongation of the hypogeal cotyledon, which assists the primary root to bore deeply into the soil and allows bulb formation within the first two months after germination (Clark & Parsons, 1994, pers. obs.).

Embryological studies (Dutt, 1962; Schlimbach, 1924; Venkateswarlu & Lakshmi, 1978) have shown that the mass attained by Amaryllideae seeds is due either to the development of the ovule's solitary integument or to the endosperm. Consisting of up to 25 cell layers, the single integument in Amaryllidinae (except *Amaryllis*) is well developed relative to the endosperm (Fig. 4B). As first reported by Schlimbach (1924), stomata are present in the testa (Fig. 4D), and the integument has considerable amounts of chlorophyll and starch (Fig.

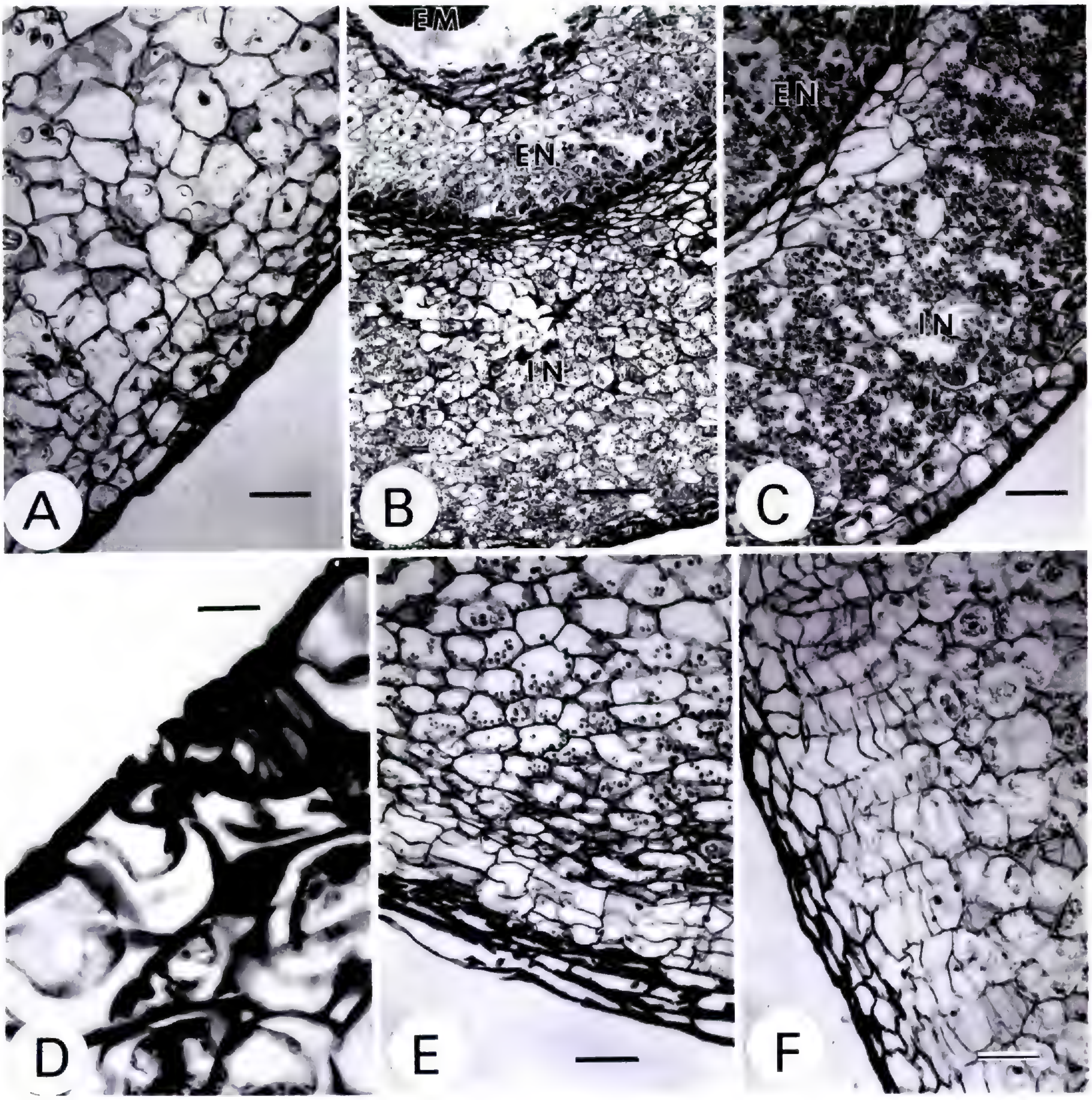

Figure 4. Seed anatomy in Amaryllideae. A–D. Species in subtribe Amaryllidinae.—A. *Amaryllis belladonna*; note the cells of the endosperm containing plastids and the partially disintegrated integument forming the testa.—B. *Brunsvigia josephinae*; part of the embryo, endosperm, and well-developed integument.—C. *Brunsvigia radula*; part of the endosperm and integument densely packed with starch grains.—D. *Strumaria chaplinii*; outer layers of integument showing chloroplasts and a stoma in cross section. E, F. Species in subtribe Crininae.—E. *Cybistetes longifolia* (*Duncan 81*); endosperm showing mature cork and phellogen surrounding the inner layers of starch-filled cells.—F. *Ammocharis coranica*; endosperm with phellogen and cork in the outer layers; note chloroplasts and starch grains in the inner cells. Scale bars: A, C, E, F = 100 μm; B = 250 μm; D = 25 μm. EM = embryo, EN = endosperm, IN = integument. Appendix I gives details of voucher specimens.

4B, C). The stomata are anomocytic (Fig. 5B–E) and the suprastomatal cavity is overarched by lobes of the adjacent epidermal cells. The epidermis is covered by a thick, sculptured cuticle (Fig. 5D, E) in which the striations become increasingly sinuous with age. Growth of the embryo is delayed during the development of the accessory seed tissues (Goebel, 1932; Schlimbach, 1924), and the embryo remains small relative to that of Crininae when the seed is shed. *Amaryllis*, with its large, irregular, white to pink seeds, is exceptional in the tribe in that it has chlorophyll only in the embryo. The seed of *Amaryllis* possesses mainly endosperm (Hofmeister, 1861), without noticeably large amounts of starch (Fig. 4A), and the integument provides only the testa (Schlimbach, 1924), which lacks stomata (Fig. 5A).

In contrast, the solitary integument and nucellus

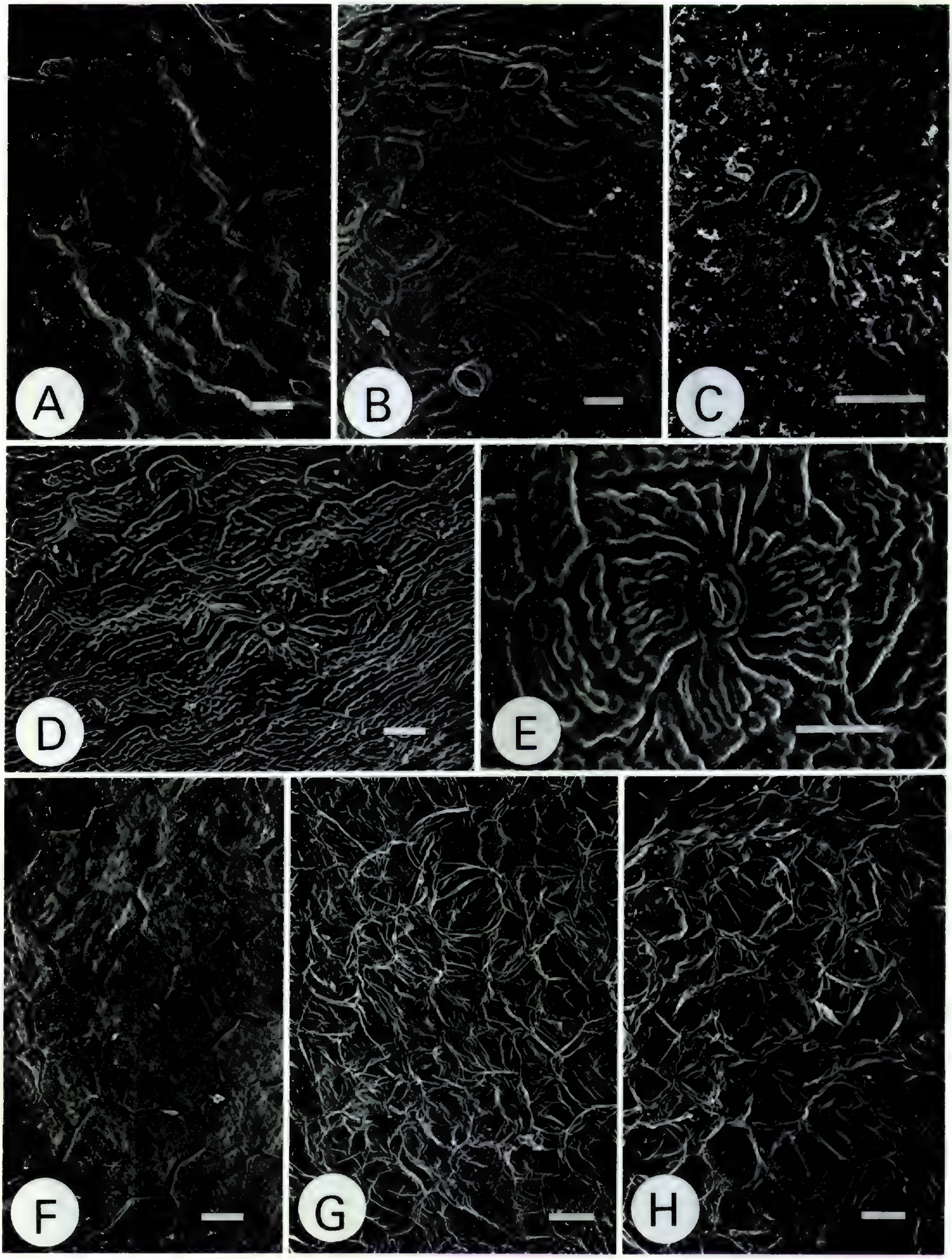

Figure 5. Seed surfaces in Amaryllideae. A–E. Species in subtribe Amaryllidinae; note the presence of stomata except in *Amaryllis*.—A. *Amaryllis belladonna*.—B. *Brunsvigia orientalis*.—C. *Nerine filifolia*.—D. *Strumaria truncata*.—E. *Hessea breviflora*, showing detail of the thick sinuous cuticle. F–H. Species in subtribe Crininae; note the corky surface at different stages of maturity.—F. *Boophone disticha*.—G. *Crinum variabile*.—H. *Ammocharis coranica*. Scale bars: 50 μm. See Appendix I for details of voucher specimens.

of Crininae are transitory and absent from the fully developed seed (Dutt, 1962, 1970). The mature seed consists of massive amounts of starch-containing endosperm. The endosperm is differentiated into cork in the outermost layers (Fig. 5F–H) and has several layers of chlorophyll-containing cells immediately below the phellogen (Fig. 4E, F). The seeds of Crininae are larger (10–30 mm diam.), more irregular and angular than the ovoidal, stomatose seeds (4–10 mm diam.) of the Amaryllidinae. The embryo is well developed when the seed is shed, and the orientation of the embryo with respect to the seed as a whole is arbitrary (Toilliez-Genoud, 1965). Cotyledon extension is positively geotropic even within the seed (Howell & Prakash, 1990).

The chlorophyllous tissue present in the integument of the *Nerine–Brunsvigia–Crossyne–Hessea–Carpolyza–Strumaria* clade and in the outer layers of the endosperm in Crininae implies some functional activity. Tests with infrared gas analysis showed that seeds of representatives from both subtribes (*Brunsvigia orientalis* (L.) Eckl. & Zeyh. and *Cybistetes longifolia* (L.) Milne-Redh. & Schweick.) are photosynthetically active and that those with a well-developed integument are capable of photosynthesis at lower light levels than those of Crininae (Wand, pers. comm.). Furthermore, a test for durability in water indicated that seeds of *C. defixum* Ker Gawl. and *C. flaccidum* Herbert had unimpaired germination when removed from fresh water after four months (Clark & Parsons, 1994; Dutt, 1962), although fresh water increases susceptibility to pathogen invasion (Manasse, 1990), and when wounded, the damaged outer portions of *Crinum* seeds rapidly produce fresh cork tissue (Dutt, 1962; Merry, 1937). Tests on the buoyancy and viability of *Crinum* seeds in salt water indicate that they can float and remain viable for more than two years (Koshimizu, 1930).

The phylogeny generated by the morphological data reveals little about the character assembly of the three seed types that exist in Amaryllideae. All the seed characters for Crininae (characters 31 and 32, Fig. 2) appear at the same branch point of the phylogeny; similarly, the seed characters for *Nerine*, *Brunsvigia*, *Crossyne*, *Hessea*, *Carpolyza*, and *Strumaria* resolve at a single node (characters 28, 29, and 30, Fig. 2). In general, this pattern suggests that the selective association between these characters is strong (Armbruster, 1992; Frumhoff & Reeve, 1994), but, in the absence of additional data, our interpretation remains tentative. Relative to the bitegmic ovule and dry seeds of the outgroup, it is evident that the unitegmic ovule and fleshy seeds of Amaryllideae arose at the base of the lineage, through the loss of an integument in the ovule and the loss of the metabolic activity that leads to maturation drying in the seed. The solitary integument persisted and thickened in the seeds of the Amaryllidinae lineage, and chlorophyll and stomata developed. In Crininae, the integument became short-lived and disappeared from the seed, but abundant endosperm and a corky covering were developed. Thus, apart from a major divergence in seed morphology subsequent to the origin of the fleshy, nondormant seed in Amaryllideae, no prevailing sequences in the origin of the different seed characters are evident.

EVOLUTION OF DISPERSAL SYSTEMS IN AMARYLLIDEAE

Wind dispersal (anemochory) occurs in six genera of Amaryllideae (Fig. 6), and in all but one of these clades the mode of wind dispersal is anemogeochorous (sensu Van der Pijl, 1982). The functionally interrelated characters shared by the five anemogeochorous taxa are low stature, lightness of the infructescence; detachment of the infructescence as a single unit before seed release (characters 22(2) and 23, Fig. 2); and long, stiff pedicels (character 9, Fig. 2) that radiate outward in all directions. Despite the similarities in the morphology and manner in which the infructescences of each genus are blown over the ground, subtle differences are evident in the dispersal units' structure and tumbling, skidding, or lofting ability.

Particularly good tumblers have been observed among representatives of the *Brunsvigia–Crossyne* clade. In many *Brunsvigia* species this ability appears to be associated with broad, kitelike capsule surfaces (Fig. 7A, B), a characteristic that is recognized to be optimal for ease of rolling (Maddox & Carlquist, 1985; Van der Pijl, 1982). This specialization is further enhanced by the tardy dehiscence of the capsules, which prolongs the period over which seed is scattered. In *Crossyne* the infructescences are uniformly spherical due to the exceptionally large number of pedicels (100 or more), and these equal the scape in length (Fig. 7C). When released, contact with the ground is minimal and little force is required to roll the ball-like infructescence.

Relative to other representatives of Amaryllideae, *Hessea*, *Carpolyza*, and *Strumaria* are characteristically diminutive in size. The narrowly distributed, wind-dispersed species of *Hessea* and *Strumaria* subg. *Gemmaria* have infructescences in which the pedicels often remain shorter than the scape (ca. half the length of the scape) and are few

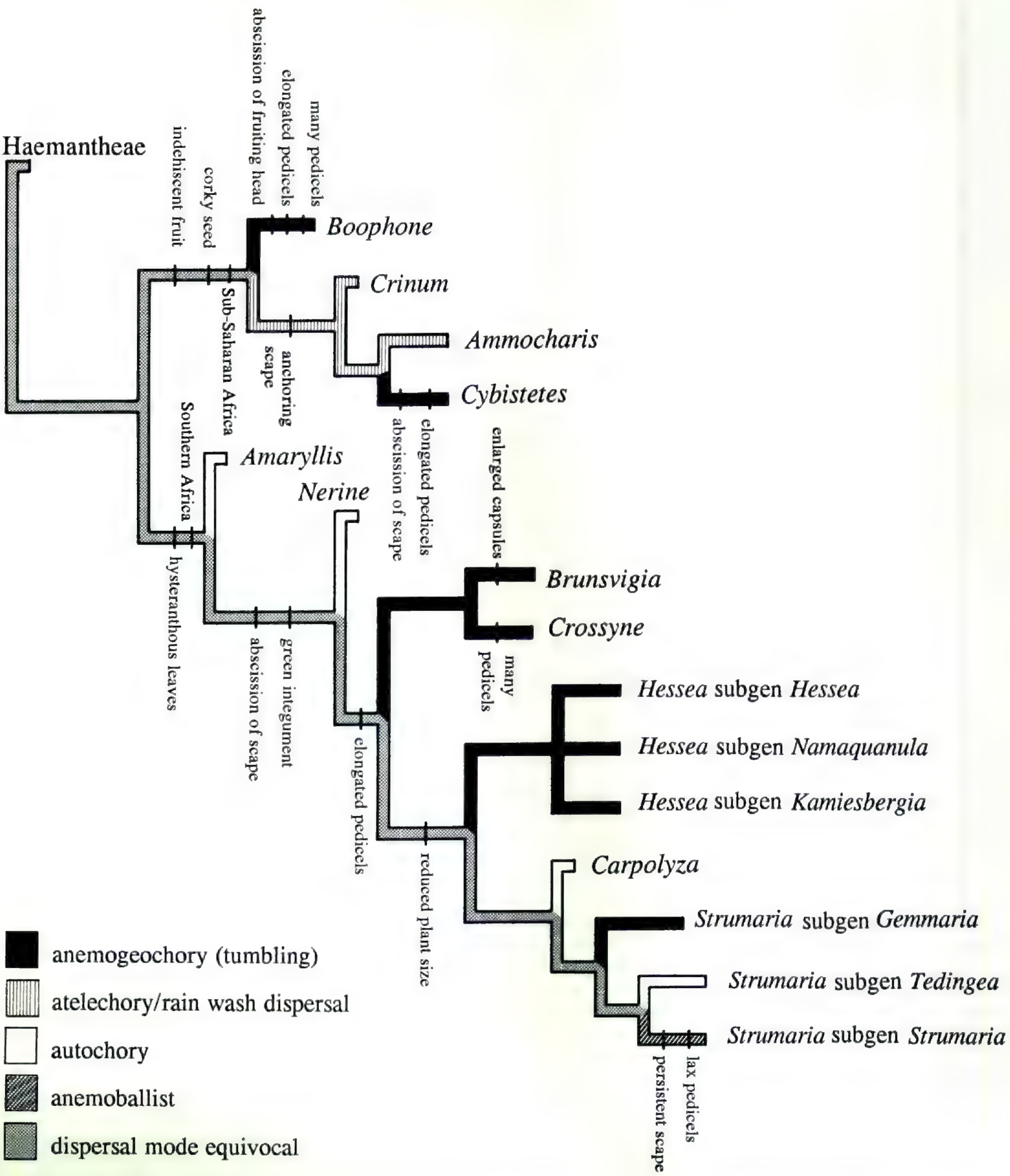

Figure 6. Dispersal systems, plant phenology, phytogeography, and functionally related seed and fruit characters in Amaryllideae mapped onto the cladogram given in Figure 2.

in number. Although this configuration has some wind dispersal ability, it appears to be optimal for lodging in rock crevices and damp depressions, and in some species (*H. monticola* Snijman, *H. cinnamomea* (L'Hérit.) Durand & Schinz, and *H. mathewsii* W. F. Barker) the infructescences have been observed to interlock so that the seeds are locally concentrated (Fig. 7D).

In *Boophone* sensu stricto the more or less spherical shape of the infructescence is attained by the rapid elongation of the large number of pedicels after anthesis (Fig. 7G). Thereafter (ca. six weeks), the dried fruiting head breaks away from the top of the scape (character 23, Fig. 2) and is lofted or blown horizontally by the wind. Since the scape remains attached to the bulb, the cohesiveness of the released fruiting head is weakened and it may break into subunits before lodging. The seeds, held by the indehiscent dry fruits, are gradually released as the papery walls disintegrate during transport.

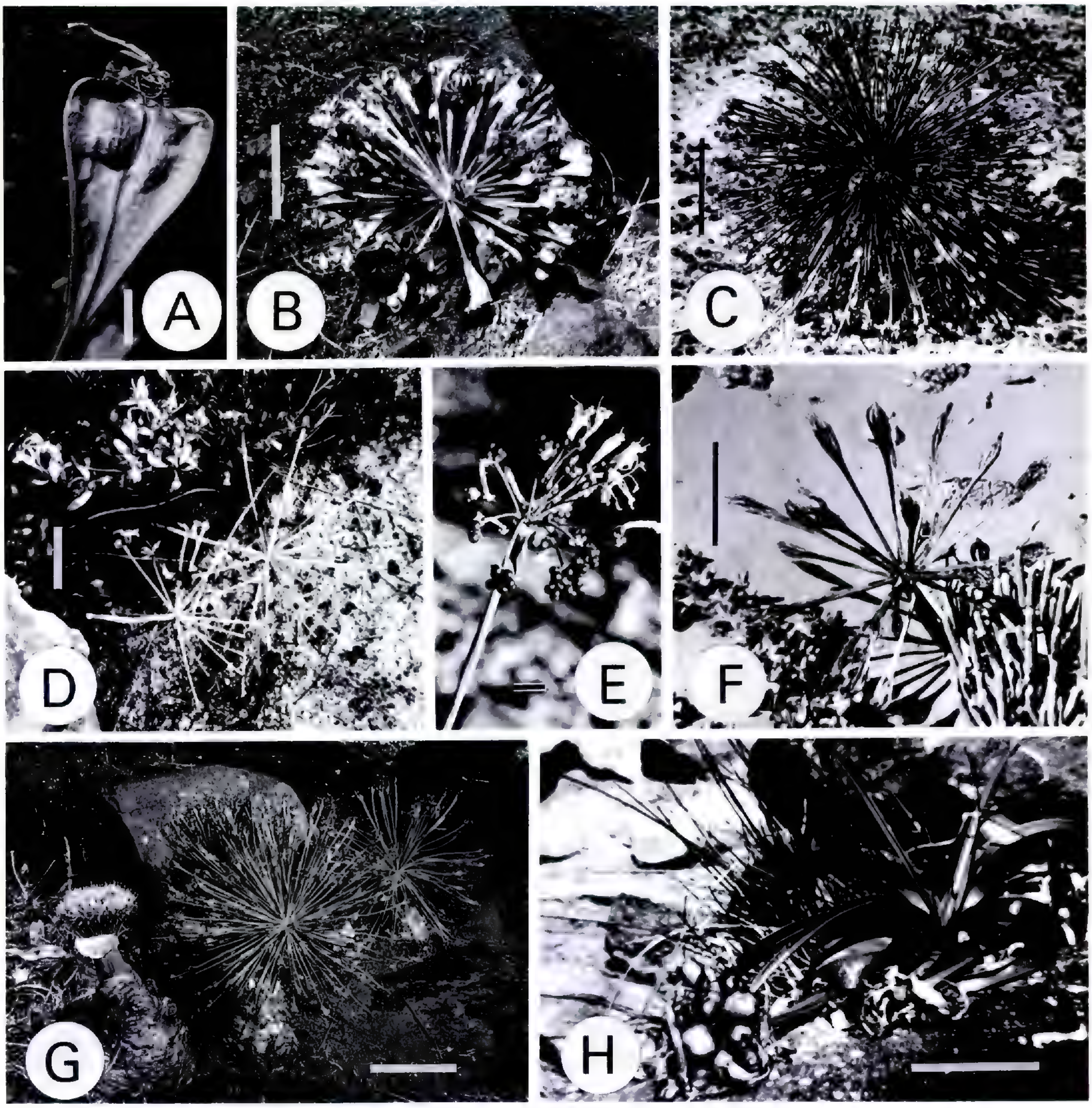

Figure 7. Infructescences of various South African winter-rainfall species of Amaryllideae.—A, B. *Brunsvigia bosmaniae*; detail of kitelike capsule, wind-blown infructescence.—C. *Crossyne flava*; intact infructescence showing the numerous, symmetrically arranged pedicels.—D. *Hessea monticola*; detached, interlocked infructescences each with few pedicels.—E. *Strumaria truncata*; note the lax, pendulous pedicels.—F. *Cybistetes longifolia*; a wind-rolled infructescence showing frayed, worn-down fruits.—G. *Boophone haemanthoides*; note the elongation of the pedicels after flowering.—H. *Crinum variabile*; showing the mature fruits dropped close to the parent plant. Scale bars: A, E = 1 cm; B–D, F–H = 10 cm.

The infructescence configuration of *Cybistetes* is essentially similar to that of many *Brunsvigia* species; however, the indehiscent, protective, strongly ribbed, dry fruits are dependent on being worn down by rolling (Fig. 7F), a process that gradually releases the seeds.

From the character distribution, the secondary loss of the abscission zone in the scape, and a reversal to short, lax pedicels (characters 9 and 22(0), Fig. 2) have apparently given rise to one further method of wind dispersal in representatives of *Strumaria* subg. *Strumaria*. In this group the fruiting head does not detach and the seeds are individually released relatively high above the ground surface. The pedicels in *S. truncata* Jacq., *S. barbarae* Oberm., and *S. hardyana* D. & U. Müll.-Doblies are flexible and pendulous and swing to and fro in strong winds so that seeds are widely scattered from the parent plant (Fig. 7E). Unlike the secondary transportation of the seed in other wind-dispersed Amaryllideae, the trajectory of the seed in *Strumaria* subg. *Strumaria* is direct from plant to

ground, and belongs to the dispersal class of anemoballists (Van der Pijl, 1982).

The sequence of character assembly in the phylogeny suggests that the development of anemogeochory in Amaryllidinae possibly commenced with the hysteranthous leaf habit, which is almost basal to the subtribe (Fig. 6), followed by the development of an abscission layer in the scape at ground level and thereafter by an inflorescence with long pedicels (Fig. 6). In combination, these characters appear to have resulted in the shedding of the infructescence at a time when the effect of the vegetative cover as a potential windbreak was minimal, and with a configuration that could have supported the transition of the entire infructescence into a single, complex unit, in which other characters associated with wind dispersal could be independently derived. These further specializations (Fig. 6) mostly reflect small quantitative changes: increased capsule surface (*Brunsvigia*), increased pedicel number (*Crossyne*), and altered pedicel length (*Brunsvigia, Crossyne, Hessea,* and *Strumaria*).

In contrast, neither hysteranthous leaves nor an abscission zone in the scape are basal to subtribe Crininae. The apparent absence of an historical transition toward the light, spherical, detaching infructescences of *Boophone* and *Cybistetes* (Fig. 6) suggests that the assembly of characters suited to anemogeochory in these two lineages was extremely rapid, or that the intermediate ancestral species are extinct. The differences in the situation of the abscission zone in the scape of *Boophone* sensu stricto and *Cybistetes* (at the top of the scape and at ground level, respectively) imply that the dispersal units of these genera are independently derived structures. This indicates that anemogeochory evolved twice in Crininae. The interpretation for Amaryllidinae, however, remains ambiguous. Two equally parsimonious hypotheses can be proposed. Either anemogeochory evolved independently in three lineages of Amaryllidinae (in the *Brunsvigia–Crossyne* clade, the *Hessea* clade, and in *Strumaria* subg. *Gemmaria*); or anemogeochory evolved only once in the *Brunsvigia–Strumaria* clade and was subsequently lost in *Carpolyza* and in the *Strumaria* clade consisting of subgenera *Strumaria* and *Tedingea.* Either interpretation, however, suggests that the fruiting characters associated with wind dispersal are plastic.

Dispersal by tumbling is restricted to and consistently present in the five genera and one subgenus of *Strumaria* that we have discussed. With the exception of only *Boophone,* all are confined to southern Africa and, with the exception of some *Brunsvigia* and *Strumaria* species, all are concentrated in the western half of South Africa. The highest concentrations of Amaryllideae species with the anemogeochorous habit (based on the number of species recorded in BOL, NBG, PRE, and SAM per 15′ × 15′ grid area) are in the west of the Northern Cape (grid 3119AC, eight species), Namaqualand (grids 2917BA, 3017BB, 3118DA, and 3118DB, five species each), and the Western Cape (3319CB, six species; 3420BC, five species). This clearly indicates that wind dispersal in Amaryllideae is more common in South Africa than in the rest of Africa and that the semiarid, winter-rainfall region has the greatest diversity of wind-dispersed representatives.

Ellner and Shmida (1981) found similarly high concentrations of taxa adapted to tumbling in the semi-desert areas of Israel, and Maddox and Carlquist (1985) reported wind dispersal in many Californian desert plants. Van der Pijl (1982) stressed the association between wind dispersal and biotic poverty, particularly in pioneer vegetation, whereas the studies of Maddox and Carlquist (1985) concentrated on the importance of wind in determining the dispersal mode of desert plants. The winter-rainfall region of southern Africa encompasses two biomes (Rutherford & Westfall, 1986) in which wind and disturbance are major features. The Fynbos Biome offers numerous transient niches through frequent fire (Cowling, 1987) and the Succulent Karoo Biome, with a 15–50% canopy cover (Hilton-Taylor, 1994), offers many more persistently open sites. Wind in both biomes is reported to exceed that of similar climatic regions elsewhere in the world (Deacon et al., 1992).

The other major dispersal specialization in Amaryllideae is represented in the *Crinum–Ammocharis* clade (Fig. 6), where the seeds are large, the fruits are variable, and the infructescences have no wind dispersal ability. Most species of *Crinum* and *Ammocharis* have green and membranous to brown and papery fruits; however, the fruit walls of a few tropical species of *Crinum* (*C. delagoense* I. Verd., *C. kirkii,* Baker, *C. papillosum* Nordal, and *C. stuhlmanii* Baker) are berrylike with a red to orange, thick or spongy pericarp (Nordal, 1982). This trend corresponds with Dahlgren and Rasmussen's (1983) hypothesis that baccate fruits in Amaryllidaceae are secondarily derived. The somewhat lax scapes and short pedicels of these genera, whose representatives commonly occupy washes, salt pans, or streambeds (Table 3), do not detach from the bulb. After anthesis the scape elongates, bends downward, and either rests on the ground (Fig. 7H) or droops into water. Until the walls grad-

ually disintegrate, the seeds are retained in the indehiscent fruit close to the parent plant. Depending on local conditions, the angular seeds germinate where they were deposited or their buoyancy allows them to be carried into seasonal washes and stream beds or the floodplains of permanently flowing rivers (Clark & Parsons, 1994; Manasse, 1990, pers. obs.).

Limited dispersal has been regarded either as a strategy to recapture a favorable site where suitable habitats are limited (Zohary, 1962) or alternatively as a product of specialized seed-containers which serve primarily to protect and regulate the timing of dispersal and germination (Ellner & Shmida, 1981). The loss of an opening mechanism in the fruit at the base of the Crininae lineage (character 24, Fig. 2) and the development of a large seed with a specialized endosperm at the same point of the phylogeny (characters 31 and 32, Fig. 2) suggest an early evolutionary association between the indehiscent fruit and the large seeds in Crininae. The subsequent development of the anchoring function by the persistent, lax scape in *Crinum* and *Ammocharis* (Fig. 6) suggests, therefore, that temporal limitation preceded spatial limitation of seed dispersal in Crininae. A critical analysis of the evolutionary sequence of dispersal and protective functions nevertheless awaits tests on the role that the berrylike fruits of *Crinum* may play in protecting the developing seeds from possible microbial damage in moist subtropical or tropical terrestrial habitats (see Corner, 1992).

The presence of both wind- and water-dispersal mechanisms in Crininae indicates greater diversity in dispersal mode in Crininae than in Amaryllidinae. Since particularly large, endosperm-rich seeds are basal to the Crininae lineage, this pattern supports the hypothesis (Stebbins, 1970) that taxa having large seeds are particularly subject to selection pressures favoring special mechanisms for seed dispersal. Although Clark and Parsons (1994) suggested that ravens may carry and drop seeds of *Crinum flaccidum,* biotic dispersal of the fleshy seeds has never been recorded in the tribe. The large, water-rich seeds of Amaryllideae, which are borne near the ground and dropped at or near maturity, have no smell (pers. obs.). Except in *Amaryllis,* the seeds lack attractive coloring and none require burial for germination (Isaac & McGillivray, 1965; Rendle, 1901, pers. obs.). These characteristics match none of the syndromes that Van der Pijl (1982) has identified as adaptive for biotic dispersal. It seems possible that the highly toxic alkaloids, which are widely present in the tribe (see Watt & Breyer-Brandwijk, 1962), may have limited seed predation (see Manasse, 1990) and the development of seed and fruit specializations primarily associated with reptile, bird, or mammalian dispersal agents, and conversely, may have promoted the tribe's evolutionary development toward the exploitation of diverse abiotic dispersal mechanisms.

EVOLUTIONARY PATTERNS IN THE ECOLOGY OF AMARYLLIDAEAE

It is well accepted that new periods of evolutionary vigor and new diversification coincide with the conquest of new biological niches, by means of new features (Riedl, 1978). Characters that permit a fairly rapid departure of a group of organisms from a preceding ecological sphere are referred to as key innovations by Larson et al. (1981). Moreover, such innovations are considered to promote the appearance of supportive adaptations during the ecological transition.

The developmental stage at which selective pressures would be expected to be maximal is that of early seedling development (Stebbins, 1974). Thus for Amaryllideae we suggest that seedling vigor, associated with the green embryo of the large non-dormant seed, probably contributed to the widespread radiation of many ancestral species of the group throughout sub-Saharan Africa during the early Tertiary when seasonally moist subtropical/tropical conditions prevailed (see Axelrod & Raven, 1978). With the subsequent aridification of Africa and the inception of extreme summer-aridity in southwestern Africa during the Pliocene (Deacon et al., 1992; Tankard & Rogers, 1978), a postulated key innovation for Amaryllidinae was the development of a seed with a large, green integument and stomatose testa. Since the integument is thought to enable the seed to photosynthesize and ripen independently of the parent plant (Goebel, 1932), this novel feature of post-ripening is considered to have facilitated the accelerated shedding of the infructescence, and so promoted the transition of the entire infructescence into a unit, highly specialized for wind dispersal (Fig. 6). This occurred especially in the semiarid, winter-rainfall region of southwestern Africa where the short growing season favored the seed's rapid release to coincide with the onset of the rainfall season, and the extreme winds favored the development of anemogeochory.

With increasing aridity the phylogenetic hypothesis for Crininae reflects a different evolutionary strategy. The subtribe's present distribution suggests that the evolution of its large seed was mainly promoted in the summer-rainfall regions of sub-Saharan Africa, where the duration of the growing

season imposed little limitation on seed size. *Boophone* and *Cybistetes* adapted to dry, open sites, but many species of *Crinum* and *Ammocharis* adopted a hydrophilic habit that allowed them to survive at the margins of permanent and seasonal water bodies. A key innovation that possibly permitted Crininae to evolve both xerophilic and hydrophilic habits was the development of a protective, ecologically versatile, corky seed covering, whose water-resistant and insulating qualities led to the evolution of wind- and water-dispersal mechanisms (Fig. 6) during the climatic changes of the Pliocene. The occurrence, however, of only three wind-dispersed Crininae species in the winter-rainfall of southwestern Africa area may reflect an intrinsic constraint to the production and timely release of the lineage's large seeds in a region where the growing season is short. Furthermore, although the pantropical distribution of *Crinum* may reflect a former Gondwanan distribution, the development of water dispersal and the tolerance of *Crinum* seeds for saline conditions supports Koshimizu's (1930) and Arroyo and Cutler's (1984) suggestion that long-distance dispersal events may have been influential in the past. We propose that the concentration of a great number of *Crinum* species in southern Africa (Nordal, 1977; Verdoorn, 1973) is a consequence of its atelechorous/rain wash dispersal mechanism which, together with the inability to develop stored seed banks, resulted in high rates of isolation, migration, and extinction among the ancestral taxa inhabiting the seasonal water systems in the increasingly arid regions of the west.

Conclusion

Character distribution in the Amaryllideae indicates constancy in floral and vegetative morphology relative to the diversity shown in the seed and fruiting structures. Seed characters have been shown to have greatest diagnostic value at the tribal and subtribal level. A single integument, at least at some stage of the seed's development, and a green embryo are synapomorphic for the tribe. Large cork-covered, green, endosperm-rich seeds characterize Crininae, and seeds with a green, stomatose integument are characteristic of all Amaryllidinae other than *Amaryllis*. Elsewhere in Amaryllidaceae, fleshy seeds also occur in the African tribe Haemantheae and the mainly American tribe Eucharideae, but so far little is known about their phylogenetic importance or ecology (Meerow, 1989). In contrast, the phylogeny of Amaryllideae, combined with data on dispersal, germination, and distribution patterns, suggests that much of the diversification in Amaryllideae arises from the group's novel seed characters. We propose that the specialized seed morphology and the unique and complex dispersal systems in Amaryllideae reflect a series of altered compromises that developed during the climatic changes of the past; in particular between the selection pressures that favored large, nondormant seeds, and those that favored diverse but efficient modes of seed dispersal. The seed-dispersal mechanisms that have evolved in Amaryllideae are all associated with abiotic agents, predominantly wind and water, whereas biotic dispersal remains unknown in the tribe.

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Appendix I. Amaryllideae material examined for seed micromorphology. Vouchers marked with an asterisk were also used for infrared gas analysis.

Amaryllis belladonna L., South Africa, Vredenburg, *Snijman 848* (NBG); *Ammocharis coranica* (Ker Gawl.) Herb., South Africa, Bloemfontein, *Müller 415* (NBG).

Boophone disticha (L.f.) Herb., South Africa, Montagu, *Snijman 1268* (NBG); *Boophone haemanthoides* F. M. Leight., South Africa, Nieuwoudtville, *Snijman 588* (NBG); *Brunsvigia bosmaniae* F. M. Leight., South Africa, Karkams, *Snijman 275* (NBG); *Brunsvigia comptonii* W. F. Barker, South Africa, Laingsburg, *Snijman s.n.* (NBG 151858); *Brunsvigia josephinae* (Redouté) Ker Gawl., South Africa, Worcester, *Compton 20484* (NBG); *Brunsvigia litoralis* R. A. Dyer, South Africa, Jeffreys Bay, *Malan 137* (NBG); *Brunsvigia minor* Lindl., South Africa, farm Arendskraal, *Snijman 596* (NBG); **Brunsvigia orientalis* (L.) Eckl. & Zeyh., South Africa, near Vanrhynsdorp, *Snijman 437* (NBG); *Brunsvigia radula* (Jacq.) W. T. Aiton, South Africa, Knersvlakte, *Snijman 1254* (NBG).

Crinum variabile (Jacq.) Herb., South Africa, Bowesdorp, *le Roux s.n.* (NBG 892/82); *Crossyne guttata* (L.) D. & U. Müll.-Doblies, South Africa, Montagu, *Snijman 1269* (NBG); *Crossyne flava* (W. F. Barker ex Snijman) D. & U. Müll.-Doblies, South Africa, Grootvlei, *Perry 1126* (NBG); **Cybistetes longifolia* (L.) Milne-Redh. & Schweick., South Africa, Beauvallon, *Williamson 4637* (NBG); *Cybistetes longifolia* (L.) Milne-Redh. & Schweick., South Africa, Gordon's Bay, *Duncan 81* (NBG).

Hessea breviflora Herb., South Africa, Arabies, *Williamson 3431* (NBG); *Hessea mathewsii* W. F. Barker, South Africa, farm Skaapplaas, *Snijman 842* (NBG); *Hessea pusilla* Snijman, South Africa, farm Perdekraal, *Snijman 1072* (NBG); *Hessea stenosiphon* (Snijman) D. & U. Müll.-Doblies, South Africa, Kamiesberg, *Snijman 1179* (NBG).

Nerine bowdenii W. Watson, South Africa, Harrismith, *Schelpe s.n.* (NBG 878/75); *Nerine filamentosa* W. F. Barker, South Africa, Cathcart, *MacMaster s.n.* (NBG 148/85); *Nerine filifolia* Baker, South Africa, Harrismith, *Schelpe s.n.* (NBG 877/75); *Nerine marincowitzii* Snijman, South Africa, SE of Leeu-Gamka, *Snijman 1245* (NBG); *Nerine masonorum* L. Bolus, South Africa, near Mquanduli, *Cannon & Mason s.n.* (NBG 66355); *Nerine undulata* (L.) Herbert., South Africa, Engcobo, *Gibson s.n.* (NBG 59983).

Strumaria aestivalis Snijman, South Africa, Langberg, *Perry 1991* (NBG); *Strumaria chaplinii* (W. F. Barker) Snijman, South Africa, Paternoster, *Barker 10239* (NBG); *Strumaria gemmata* Ker Gawl., South Africa, Baviaanskloof, *Vlok 956* (NBG); *Strumaria karooica* (W. F. Barker) Snijman, South Africa, Sutherland, *Forrester & Leitch s.n.* (NBG 145851); *Strumaria karoopoortensis* (D. & U. Müll.-Doblies) Snijman, South Africa, Fonteinskop, *Perry 1278* (NBG); *Strumaria pygmaea* Snijman, South Africa, farm Kersbosvlei, *Snijman 862* (NBG); *Strumaria tenella* (L.f.) Snijman subsp. *orientalis* Snijman, South Africa, Bloemfontein, *Oliver 313* (NBG); *Strumaria truncata* Jacq., South Africa, Steinkopf, *Perry 1057* (NBG).

A TAXONOMIC SYNOPSIS OF THE GENUS *SALSOLA* (CHENOPODIACEAE) IN NORTH AMERICA[1]

Sergei L. Mosyakin[2]

ABSTRACT

A key and synopsis of the genus *Salsola* L. (Chenopodiaceae) in North America north of Mexico are presented, including the taxonomy and distribution of six recognized species. A new combination is proposed: *Salsola kali* L. subsp. *pontica* (Pallas) Mosyakin.

The genus *Salsola* L. sensu lato, which includes the segregate genera *Caroxylon* Thunberg, *Climacoptera* Botschantsev, *Hypocylix* Woloszczak = *Darniella* Maire, *Neocaspia* Tzvelev, *Nitrosalsola* Tzvelev, and *Xylosalsola* Tzvelev, comprises 130–150 species, which are especially numerous in the arid and coastal zones of Eurasia, including Central Asia (all sections of the genus), the Middle East, and the Mediterranean region. Some species, mostly representatives of *Salsola* sect. *Salsola* (including sect. *Kali* Dumortier), also occur in other regions of the world as introduced synanthropic weeds, including in North America.

The considerable biological diversity of arborescent and shrubby species of *Salsola* sect. *Caroxylon* (Thunberg) Fenzl (or the separate genus *Caroxylon*) is confined also to northern (Mediterranean), southern, and eastern parts of Africa (see Botschantzev, 1969, 1975a, b). Some "satellite" genera closely related to *Salsola* (*Aellenia* Ulbrich, *Physandra* Botschantzev, *Horaninivia* Fischer & Meyer, *Girgensohnia* Bunge) are widely recognized by botanists, while some others are not. However, in most cases the latter segregate genera, usually treated as synonyms of *Salsola* sensu lato or recognized as infrageneric taxa, are not less distinct from *Salsola* sensu stricto, than, for example, such readily accepted pairs of genera as *Kochia* Roth and *Bassia* Allioni, *Salicornia* L. and *Arthrocnemum* Moquin-Tandon, *Corispermum* L. and *Anthochlamys* Fenzl, *Atriplex* L. and *Halimione* Aellen. It means that the generic boundaries of *Salsola* and related taxa are in need of a systematic revision. It is also evident that *Salsola* in the traditional sense should be regarded as a group of genera, rather than as a natural genus. The taxonomic problems related to forming a generic concept within this group have been discussed recently by Tzvelev (1993). He accepted several quite distinct genera, including *Caroxylon*, which is represented in North America by only one alien species, usually referred to as *Salsola vermiculata*; all other North American taxa belong to *Salsola* sensu stricto.

As noted above, all species of North American *Salsola* should be regarded as naturalized or casual aliens native to Eurasia.

In the course of preparing a taxonomic treatment of the genus for the *Flora of North America* it has become evident that the taxonomy, nomenclature, and distribution of some species need clarification. Extensive herbarium collections from MO, GH, NY, and US served as the base for this study. Comparative Eurasian material from LE, KW, MHA, and some other Russian and Ukrainian herbaria was also examined. Types of *Salsola australis* R. Br. and *S. caroliniana* Walt. sent on loan to MO from BM were also consulted, as were photographs of Linnaean specimens from LINN.

Following is a brief synopsis of the *Salsola* species occurring in North America north of Mexico,

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with some notes on their taxonomy and distribution. Unfortunately, it is impossible to present a complete account of the North American distribution for all *Salsola* species, mostly due to taxonomic confusion (especially for species of the *S. kali* aggregate) in the literature. The distribution statements in this account are based on reliably identified herbarium specimens seen in the course of this study. For more or less common species only states, provinces, and territories are cited in the following synopsis, while for the rare aliens more detailed information is presented.

This article does not pretend to solve all problems concerning distribution and ecology of introduced species of *Salsola* in North America. Its primary aim is to provide a more reliable taxonomic background for further studies.

Taxonomy of *Salsola* in North America

Salsola L., Sp. Pl. 1: 222. 1753. TYPE: *Salsola soda* L. (lectotype, selected by Britton & Brown, 1913).

Annual herbs, or subshrubs [in the Old World also shrubs and small trees], glabrous or ± pubescent or hispid. Stems branched (very rarely simple), erect, ascending or prostrate. Leaves mostly alternate (occasionally lower ones subopposite), sessile, semiterete, lanceolate, linear, or filiform, margin entire. Inflorescences spicate. Flowers normally bisexual, solitary (rarely in twos or threes, but in this case lateral flowers poorly developed) in axils of bracts, with 2 bracteoles. Perianth segments 5, at maturity covering the fruit and in most species developing a transverse dorsal membranous or almost coriaceous wing (sometimes only 2 or 3 perianth segments winged, or all wingless). Stamens 5. Styles and stigmas 2 (3). Seeds usually horizontal; pericarp adherent; embryo spiral.

The name is derived from Latin sal, salt; or salsus, salty. The name Salsola was first used by Cesalpino (1519–1603) for a plant that is now known as *Halogeton sativus* (L.) Moquin-Tandon (basionym: *Salsola sativa* L., published in 1762).

Vernacular names. Saltwort, Russian-thistle (English); Soude, Salsovie (French); Salzkraut (German); Kali, Soda (Italian); Solyanka (Russian), Solyanka, Kurai (Ukrainian); Solanka (Polish); Slanobyl (Czech).

Artificial Key to *Salsola* Taxa in North America

1a. Annual herbs, glabrous or papillose-hispid; leaves and bracts with spinose (or at least mucronulate) apex; perianth segments completely glabrous, or indistinctly papillose (occasionally ciliate at margin).
  2a. Leaves (especially lower ones) mostly opposite, with apex mucronulate, not spinose; bracts distinctly swollen at base, alternate or subopposite; perianth segments normally with crenate or pectinate-ciliate apex; plants always glabrous ..... 5. *S. soda*
  2b. Leaves all alternate (sometimes only 1–3 pairs of lower ones subopposite), with spinose or spinescent (rarely almost mucronulate) apex; bracts not swollen, or in some species indistinctly swollen at base, normally alternate; perianth segments with acute entire apex (sometimes papillose at margins, but never crenate or pectinate-ciliate); plants papillose-hispid or occasionally glabrous.
    3a. Leaves fleshy (in living plants), linear, in herbarium specimens mostly 1–2 mm broad, ± gradually narrowed into rather firm apical spine; bracts reflexed at maturity.
      4a. Perianth segments with long-acuminate or long-subulate spinose apex, at maturity forming a slender columnar beak above the broad wings; fruiting perianth 7–12 mm diam.; plants of open sands and inland saline habitats ..... 3. *S. paulsenii*
      4b. Perianth segments with short-acuminate or triangular apex, never forming a columnar beak at maturity; wings absent or shorter; fruiting perianth 6–7(10) mm diam. or less; plants of maritime saline habitats (seashores, tidal marshes, etc.). ..... 1. *S. kali*
        5a. Perianth segments with rigid, subspinose apex and distinct midvein; bracteoles not swollen, free. ..... 1a. *S. kali* subsp. *kali*
        5b. Perianth segments with weak apex and obscure midvein; bracteoles swollen, connate at least at base. ..... 1b. *S. kali* subsp. *pontica*
    3b. Leaves normally not fleshy (occasionally somewhat fleshy in plants growing in saline and alkaline habitats), narrowly linear to filiform, in herbarium specimens mostly less than 1 mm broad, in most cases abruptly narrowed into weak apical spine (mucro); bracts reflexed or appressed at maturity.
      6a. Bracts appressed and strongly imbricate at maturity, gradually narrowed into subulate spinose apex; inflorescence narrowly spicate, rather dense, not interrupted at maturity; perianth segments wingless or rarely with narrow (usually less than 1 mm) erose wing; plants normally erect, branched above the base, or with a few slender branches near the base ..... 4. *S. collina*
      6b. Bracts reflexed, not imbricate at maturity, in most cases ± abruptly narrowed into spinose or submucronulate apex; inflorescence spicate, at maturity interrupted at least in lower half; perianth segments normally with membranous wing; plants erect or ascending, branched from the base.

7a. Perianth segments with long-acuminate spinose apex, at maturity forming a slender columnar beak above the wings; fruiting perianth 7–12 mm diam. ..... 3. *S. paulsenii*

7b. Perianth segments with obtuse to weakly acuminate or reflexed apex, at maturity not forming a columnar beak; fruiting perianth normally less than 8–10 mm diam. ..... 2. *S. tragus*

1b. Perennial subshrubs covered with glabrous (smooth) and minutely denticulate hairs (sometimes becoming glabrous at maturity); leaves and bracts obtuse, without spinose apex; perianth segments with ± pubescent (not papillose) apex. ..... 6. *S. vermiculata* sensu lato

1. Salsola kali L., Sp. Pl.: 222. 1753. TYPE: Herb. Burser XVI(2): 24 (lectotype, selected by Jonsell & Jarvis (1994), UPS not seen).

See discussion below. The species is described from Europe: "Habitat in Europae litoribus maris."

Annual herbs, 5–50 cm tall, papillose-hispid or glabrous. Stems branched from the base, erect, rarely ascending; branches arcuate or sometimes prostrate. Leaves alternate, linear, fleshy, in herbarium specimens mostly 1–2 mm broad, semiterete, normally not swollen at base; apex ± gradually narrowed into rather firm spine. Inflorescence spicate, interrupted at maturity. Bracts reflexed, not imbricate at maturity, alternate, narrowing into subulate spinose apex. Flowers normally solitary in axils of bracts or reduced upper leaves. Perianth segments glabrous, with weak or firm apex, at maturity wingless or with comparatively narrow wing (in subsp. *pontica* sometimes prominently winged), becoming connate and united with bracteole bases, or bracteoles free. Fruiting perianth ca. 3–5 (rarely up to 8) mm diam.

Chromosome number. $2n = 36$ (Bassett & Crompton, 1970).

Distribution. Native to maritime coastal areas of Europe, northern Africa, southwestern Asia; introduced and naturalized in many other coastal regions of the world, including North America. This species is represented by two (or possibly three) subspecies.

Note on lectotypification. The specimen LINN 315.1 was selected as the lectotype of *Salsola kali* by Jafri and Rateeb (1978). This specimen represents a typical form of the species. However, it lacks a Species Plantarum number, and probably was added to the Linnaean collection after 1753. Because of that this lectotypification was superseded by Jonsell and Jarvis (1994) in favor of the Burser specimen cited above. The second Linnaean specimen identified as *S. kali*, LINN 315.2, also lacks a Species Plantarum number; moreover, it seems to be identical to *S. collina* Pallas.

1a. Salsola kali L. subsp. **kali**

Stems normally papillose-hispid (var. *kali*), or rarely glabrous (var. *polysarca* G. F. W. Meyer). Bracteoles free, not swollen. Perianth segments with rigid, almost spinose apex and distinct midvein.

Habitats. Seashores, salt marshes, sandy places in coastal regions and other saline maritime habitats, very rarely in ruderal inland habitats; 0–100 m.

Distribution. Herbarium specimens were examined from the following states, provinces, and territories: FRANCE (overseas department): St. Pierre et Miquelon. CANADA: New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island, Quebec. U.S.A.: Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, South Carolina, Virginia. This subspecies possibly also occurs in the District of Columbia, U.S.A. It is native to coastal maritime regions of western and northern Europe and is naturalized in many coastal regions of the world.

1b. Salsola kali L. subsp. **pontica** (Pallas) Mosyakin, comb. nov. Basionym: *Salsola kali* var. *pontica* Pallas, Illustr. Pl.: 37. 1803. *Salsola pontica* (Pallas) A. Degen, Flora Velebitica 2: 47. 1937. TYPE: authentic specimens in BM, lectotype not selected; see discussion below.

Stems in most cases glabrous (var. *glabra* Forsskal = *Salsola pontica* var. *glabra* Tzvelev, Ukrayins'k. Bot. Zhurn. 50(1): 82. 1993), or sometimes papillose-hispid (var. *pontica*). Bracteoles swollen, connate at base. Perianth segments with weak apex and obscure midvein.

Habitats. Seashores, salt marshes, sandy places in coastal regions, rarely in ruderal inland habitats; 0–100 m.

Distribution. Herbarium specimens were examined from the following states of the U.S.A.: Alabama, California (one locality: San Nicolas Island, Lat. 33°15′N; Long. 119°30′W, U.S. Naval Radiological Defense Laboratory, near road above sand spit at 100 ft. elevation, *R. E. Foreman (No. 42)*,

E. C. Evans III, S. C. Rainey), Delaware, District of Columbia, Florida, Georgia, Louisiana, Massachusetts, Maryland, Mississippi, North Carolina, New Jersey, New York, Oregon (only one locality: on ballast grounds of Albine, Portland, 29 Sep. 1910, *W. N. Suksdorf s.n.*), South Carolina, Texas, and Virginia; this subspecies also occurs in Mexico and seems to be common in coastal regions of South America. It is native to coastal maritime regions of southern Europe, northern Africa, and southwestern Asia, northward to Great Britain, eastward to the Caspian Sea, and is locally naturalized in many coastal regions of the world.

This subspecies is closely related to *S. kali* subsp. *kali*, and in Eurasia replaces the latter on seashores of the Mediterranean, Black, Azov, and Caspian Seas. Its nomenclature is complicated and still unresolved. For a long time it was known in European botanical literature under the misapplied names *S. tragus* (sensu auct., non L.) or *S. kali* subsp. *tragus* (L.) Čelakovský (in part, excluding the type of the basionym). According to Botschantzev (1974), the southern maritime taxon of the *S. kali* aggregate is conspecific with *S. caroliniana* Walter (type at BM), which seems to be the earliest valid name at the species level. Tzvelev (1993), however, regarded *S. caroliniana* as a synonym of *S. tragus* sensu stricto. I have studied a small fragment of the type specimen of *S. caroliniana* sent as a loan to MO. This immature plant evidently belongs to *S. kali*, not to *S. tragus* sensu stricto. However, it is impossible to assign it with certainty to any subspecies of *S. kali*. Moreover, in American literature the name *S. caroliniana*, or *S. kali* var. *caroliniana* (Walter) Nuttall, was sometimes applied to other taxa of the *S. kali* aggregate. Because of this uncertainty in the proper identity of *S. caroliniana*, I selected as a basionym for the subspecies the name given by Pallas (1803) to the coastal Eurasian race of the *S. kali* aggregate. At least, this name refers to the native Eurasian taxon, as it was noted by Degen (1937) and Tzvelev (1993). When describing his *Salsola kali* var. *pontica*, Pallas (1803) had at his disposal specimens from coastal habitats of the Black Sea in the Crimea near modern Sevastopol (". . . in littore Chersonesi Tauricae crescentes pro distincta specie habuissem, nisi lectae circa Maeotin et in mediterraneis Tauriae," Pallas, 1803: 37), and probably some additional specimens from adjacent coasts of the Black and Azov Seas, where only one littoral taxon of the *S. kali* aggregate is known to occur. The description and illustration in the protologue are also diagnostic. I did not have a chance to select the lectotype among Pallas's specimens deposited at BM; however, if there are any obstacles for selecting a particular specimen at BM, the lectotypification could be based on the illustration in Pallas (1803).

In their secondary, anthropogenous areas of distribution (particularly, in North America) both subspecies of *S. kali* are often represented by convergent or deviate forms and seem to be less morphologically and geographically separated from each other than in their native Eurasian areas (e.g., North American specimens of *S. kali* subsp. *pontica* often approach *S. tragus* in having quite broad wings, a character that is not as common in Eurasian littoral plants). Due to this peculiarity of introduced plants, it would be reasonable for the purpose of nomenclatural stability to abandon some uncertain names of taxa described within the *S. kali* aggregate from various parts of the world (including *S. caroliniana* and *S. australis*; see also discussion below, under *S. tragus*).

When immature, subspecies *pontica* is almost indistinguishable from *S. kali* subsp. *kali*. Unfortunately, many specimens of *S. kali* sensu lato are represented in American herbaria by immature plants. More detailed studies using fruiting material are needed to clarify the distribution of both taxa in North America. However, *S. kali* subsp. *pontica* is certainly a more southern subspecies (in both North America and Europe), and seems to be the only race of *S. kali* occurring in littoral habitats from South Carolina to coastal Texas. It is also known from scattered localities as far north as Massachusetts. From New Hampshire to Newfoundland only subspecies *kali* seems to occur, and it is quite common as far south as Virginia, being gradually replaced southward (in Virginia and North Carolina) by subspecies *pontica*.

Both subspecies of *S. kali* were probably the first taxa of *Salsola* introduced to North America (evidently, on ship ballasts) shortly after the establishment of the first European settlements and the beginning of colonization of the continent.

Salsola kali is confined mostly to coastal saline habitats; however, it rarely occurs as introduced in ruderal inland habitats, but usually not far away from the coast.

2. Salsola tragus L., Cent. Pl. 2: 13. 1756. *Salsola kali* L. subsp. *tragus* (L.) Čelakovský, Prodr. Fl. Boehmen 2: 155. 1871 (see discussion under *S. kali* subsp. *pontica*). TYPE: LINN 315.3 (lectotype, selected here; see also Degen, 1937; Tzvelev, 1993).

Salsola australis R. Brown, Prodr. Fl. Nov. Holl. 1: 412. 1810 (emend. Botschantzev, Kew Bull. 29: 614. 1974). TYPE: "S. Australia: Nuyts Archipelago, Pe-

trel Bay, Isle St. Francis, 8 Feb. 1802 (fl. & fr.) *Good & Bauer*" (lectotype, selected by Botschantzev (1974), BM, "planta dextra").

Salsola kali L. var. *tenuifolia* Moquin-Tandon, Chenopodearum Monographica Enumeratio: 136. 1840. TYPE locality: southwestern Ukraine: "Ad Baltam [sphalm. "Balkam" -S. M.] (Besser in herb. DC.)" (holotype, probably at P not seen; isotype in the Besser memorial collection at KW).

Salsola kali L. var. *angustifolia* Fenzl in Ledebour, Fl. Ross. 3, 2: 798. 1851. TYPE: no reference to the type in the protologue; original specimens annotated by Fenzl at LE, lectotype not selected.

Salsola kali L. var. *leptophylla* Bentham, Fl. Austral. 5: 207. 1870. TYPE locality: "Queensland and N. S. Wales." TYPE: not designated.

Salsola tragus subsp. *iberica* Sennen & Pau, Bull. Acad. Intern. Geogr. Bot. (Le Mans), ser. 3, 18: 476. 1908. *Salsola iberica* (Sennen & Pau) Botschantzev, Bot. Zhurn. (Leningrad) 54: 991. 1969, cum auct. "Sennen et Pau" (comb. invalid.). *Salsola iberica* (Sennen & Pau) Botschantzev ex Czerepanov, Svod Dopolneniy i Izmeneniy k "Flore SSSR": 192. 1973, cum auct. "Sennen et Pau." TYPE: "Hab. Castille: Miranda de Ebro (Elias); Logroño, terrains vagues, près la station (Sennen)" (holotype, not seen; isotype, US).

Salsola kali L. var. *pseudotragus* G. Beck in Reichenbach, Icon. Fl. Germ. Helv. 25: 172. 1909. TYPE: not designated; described from Germany, "Inprimis in terris interioribus."

Salsola pestifer A. Nelson in Coulter's New Manual Bot. Centr. Rocky Mountains, ed. 2: 169. 1909. TYPE: "The now widely distributed Russian Thistle" (no collection cited in protologue; authentic specimens at GH, NY, US; lectotype not selected).

Salsola ruthenica Iljin in B. A. Keller et al., Sornye Rasteniya SSSR (Weeds of the USSR), 2: 137. 1934, nom. illegit. *Salsola kali* L. subsp. *ruthenica* Soó in Soó et Jávorka, Magyar Növ. Kéz. 2: 786. 1951. TYPE: not designated.

Salsola kali L. var. *austroafricana* P. Aellen, Mitteilungen der Botanischen Staatssammlung München 4: 27. 1961. TYPE: Südwestafrika: Distr. Lüderitz-Süd, weed in dry riverbed near farmhouse farm "Klein Aus," 28.6.1949, *Kinges 2297* (M not seen). [I follow the synonymy of Botschantzev, Kew Bull. 29: 614. 1974].

Annual herbs, (5–)10–100 cm, glabrous or sparsely papillose-hispid. Stems profusely branched from the base or near the base (rarely simple in underdeveloped specimens), erect, rarely ascending; branches normally arcuate. Leaves alternate, filiform or narrowly linear, in herbarium specimens normally less than 1 mm broad, semiterete, not swollen at base; apex rather soft, subspinescent. Inflorescence spicate, interrupted at maturity (at least in lower part). Bracts at maturity reflexed, not imbricate; alternate, ± abruptly narrowing into mucronulate-spinose apex. Bracteoles free, or occasionally connate at base in lower flowers. Flowers solitary or rarely 2 or 3 (in the last case lateral flowers mostly abortive) in axils of bracts or reduced upper leaves. Perianth segments glabrous, with weak apex; at maturity distinctly winged; fruiting perianth ca. 4–10 mm diam.

Chromosome number. $2n = 36$ (Mulligan, 1961; Bassett & Crompton, 1970).

Vernacular names. Russian-thistle (English); soude roulante (French).

Habitats. Waste places, roadsides, cultivated fields, disturbed natural and semi-natural plant communities (e.g., coastal and riparian sands, semi-deserts and deserts, eroded slopes); 0–2500 m.

Distribution. Herbarium specimens were examined from the following states and provinces: CANADA: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan. U.S.A.: Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming. Judging from the limited number of herbarium specimens available from Alabama, Georgia, Louisiana, and Mississippi, this species seems to be rare (or undercollected) in the southeastern part of the United States. *Salsola tragus* probably also occurs in Newfoundland, the District of Columbia (it is known from the adjacent part of Maryland), and Florida; native to inland arid regions of southeastern Europe and Central Asia, and occasionally occurs as an introduced alien in some other regions of the world (naturalized in South Africa, Australia, and South and Central America).

Salsola tragus may have been first introduced to the United States in South Dakota in 1873 or 1874 in flax seed imported from Russia (Piper, 1898; Beatley, 1973; Crompton & Bassett, 1985). This noxious weed now occupies almost all its potential range in North America. However, young plants are considered to be an additional forage source for livestock in arid rangelands (Welsh, 1984).

The mature plant may break off at the stem base to form a tumbleweed (also called Rolly-polly in Australia).

The synonymy of *S. tragus* is complicated, and the correct use of some names applied to this taxon is still uncertain. For example, Botschantzev (1974), who had selected the lectotype of *S. aus-*

tralis R. Brown (deposited in BM), considered it to be conspecific with *S. pestifer* and *S. ruthenica*. Crompton (pers. comm.; see also note in Clemants, 1992), who had also studied the type, claimed it to be conspecific with *S. kali* sensu stricto. I have also studied the type of *S. australis* sent on loan to MO. The herbarium sheet contains several fragments. In my opinion, four of these fragments belong to *S. kali* subsp. *pontica*, a southern maritime race of the *S. kali* aggregate (see discussion above). However, the lectotype of *S. australis* selected by Botschantzev (1974) is the fifth fragment, which is mounted at the right side of the herbarium sheet. This fragment represents a form morphologically intermediate between *S. kali* subsp. *pontica* and *S. tragus*.

The combination *S. kali* subsp. *tragus* (L.) Čelakovský was constantly misapplied in Europe to the littoral taxon treated here as *S. kali* subsp. *pontica* (see discussion under that taxon). The authorship of the former combination was often incorrectly attributed to Nyman (Consp. Fl. Europ.: 631. 1881), who in fact validated it 10 years after Čelakovský.

In North America, this taxon was subsequently treated as *S. kali* var. *tenuifolia* (with the authorship incorrectly attributed to Tausch, who published only the name, nomen nudum), *S. pestifer*, *S. iberica* (with its authorship incorrectly attributed to Sennen & Pau, who published their taxon as a subspecies), and *S. australis*. In Europe this taxon was also known as *S. ruthenica* and *S. kali* subsp. *ruthenica* (Iljin) Soó. *Salsola ruthenica* is an illegitimate name, because, when describing his species, Iljin cited in its synonymy *S. pestifer*, the earlier valid name of the same rank. The subspecific name proposed by Soó is legitimate, but, since its basionym was illegitimate, it should be regarded as a new name (not a new combination; see ICBN article 58, Greuter et al., 1994).

Recently Tzvelev (1993) confirmed that the correct name for the widespread narrow-leaved weedy representative of the *S. kali* aggregate is *S. tragus* L., a name that had already been accepted for this taxon by Degen (1937). Judging from the photographs of the Linnaean specimen of *S. tragus* (LINN 315.3), which I selected as the lectotype, this point of view is correct. This change of a name seems to be desirable, because it would guarantee more stable nomenclature for this taxon in the future. The name *S. tragus* was used for this species by some American botanists in the 19th century, but unfortunately, most North American botanists did not resist the temptation to accept the common European misapplication of the name.

3. Salsola paulsenii D. I. Litvinov, Izv. Turkestansk. Otd. Russk. Geogr. Obshch. 4, 5: 28. 1905. TYPE: "Turkestania. Dominium Buchara. In arenosis subsalsis pr. Farab (ad fl. Amu-darja). 14 Sept. 1903. Legit *N. Androssow et M. Kolow*" (LE).

Salsola pellucida D. I. Litvinov, Herb. Fl. Ross. 49: No 2434. 1913. TYPE: "Dominium Buchara, in arenosis pr. Farab. 14 Sept. 1903 [sphalm. 1913—S. M.]. Leg. *N. Androssow*" (LE).

Annual herbs, 10–80(–100) cm, glabrous or sparsely papillose-hispid. Stems profusely branched from the base or near the base (rarely simple in underdeveloped specimens), erect, rarely ascending or prostrate; branches straight or arcuate, often almost perpendicular to the stem. Leaves alternate, filiform or linear, in herbarium specimens normally ca. 1 mm broad, but occasionally slightly broader, semiterete, not swollen at base; apex spinose. Inflorescence spicate, distinctly interrupted at maturity. Bracts at maturity strongly reflexed, not imbricate; alternate, narrowing into spinose apex. Bracteoles free or connate near the base, spreading, spinescent. Flowers solitary, or rarely 2 or 3 (in the last case lateral flowers mostly abortive) in axils of bracts or reduced upper leaves. Perianth segments glabrous, with long-acuminate spinose apex, at maturity forming a slender columnar beak above the wings, prominently winged. Fruiting perianth 7–12 mm diam.

Chromosome number. $2n = 36$ (Semiotrocheva, 1983; see fig. 3).

Vernacular name. Barbwire Russian-thistle.

Habitats. In sandy soil in disturbed natural and semi-natural plant communities (e.g., open sands, sand dunes, sandy waste places, semi-deserts and deserts, eroded sandy slopes, etc.); 0–1900 m.

Distribution. Herbarium specimens were examined from the following states: Arizona, California, Colorado, Nevada, Utah. *Salsola paulsenii* is native to southeasternmost Europe and Central Asia.

This species is confined mostly to open sands, and rarely to saline sandy habitats. It may be expected in the future in New Mexico and Texas, as well as in some Great Plains states. It was first reported from North America by Munz (1968), and the determination was made by Botschantzev. Additional details of distribution and morphology of this species have been discussed by Beatley (1973) and Fuller (1986).

Salsola paulsenii is weakly differentiated from its

allied taxon, *S. tragus* sensu stricto. The intermediate forms between them seem to be quite rare in Central Asia, but more common in southeasternmost Europe, western Kazakhstan, secondary synanthropic localities in East Europe, as well as in the United States.

4. Salsola collina P. S. Pallas, Illustr. Pl.: 34. 1803. TYPE: "in tractu collium cotaceorum inter Rhymnum et Samaram fl. a jugo Uralensi descendentium" (holotype, BM not seen).

Annual herbs, 10–100 cm, sparsely to densely papillose or hispid (rarely almost glabrous). Stems branched above the base (occasionally with slender branches near the base), erect, rarely ascending; branches straight or slightly arcuate. Leaves alternate, filiform or narrowly linear, semiterete, sometimes semi-amplexicaul at base; apex with rather soft bristle (rarely spinescent). Inflorescence narrowly spicate, not interrupted. Bracts at maturity appressed and imbricate, alternate, gradually narrowing into a subulate spinose apex. Flowers solitary or rarely 2 or 3 in axils of bracts or reduced upper leaves (sometimes flowers are also present at axils of lower leaves and branches, at maturity forming gall-like caducous balls). Perianth segments glabrous, with weak, flaccid apex; at maturity wingless or with narrow erose wing, becoming connate and united with bracteole bases; fruiting perianth ca. 3–5(7) mm diam.

Chromosome number. $2n = 18$ (Pohl & Gillespie, 1959).

Habitats. Waste places, roadsides and railway areas, cultivated fields, disturbed natural and semi-natural plant communities; 100–2000 (?) m.

Distribution. Herbarium specimens were examined from the following states in the U.S.A.: Arizona, Colorado, Iowa, Kansas, Michigan, Minnesota, Missouri, Montana, Nebraska, New Mexico, North Dakota, Texas, Utah, and Vermont.

The species is also reported from additional localities in Iowa (Schapaugh, 1958), Utah (S. L. Welsh, pers. comm.), and Canada: Ontario (possibly also in Quebec) and Saskatchewan (Crompton & Bassett, 1985). *Salsola collina* is native to southeasternmost Europe, southern Siberia, and arid regions of Central Asia; it is known as a naturalized or casual alien in some other regions of Europe and Asia.

This Asian species was reported for the first time for North America from Minnesota by Moore (1938). However, it had been collected in Kansas in 1923 (Brooks et al., 1976), but was misidentified. Later it spread to Colorado, Iowa, and Missouri (Cory, 1948; Schapaugh, 1958; Muhlenbach, 1979).

At present this species is known in North America mostly from the Great Plains region and scattered localities in other states. Recently it was also discovered in Canada (Crompton & Bassett, 1985). However, its actual distribution seems to be underestimated due to the common and constant confusion with deviate forms of *S. tragus*, which occasionally resemble *S. collina* in having narrow inflorescences and gall-like caducous flowers/fruits at the axils of lower and middle branches. In the future *S. collina* may be expected to occur within the present range of *S. tragus* throughout North America.

It was also reported as a casual alien from several countries of western and central Europe and is regarded to be established or even completely naturalized in eastern Europe (see map of its secondary distribution in Baranova & Khilova, 1990).

5. Salsola soda L., Sp. Pl. 1: 233. 1753. *Kali soda* (L.) Scopoli, Fl. Carn., ed. 2, 1: 175. 1772. TYPE: LINN 315.7 (lectotype, selected by I. Hedge in Jarvis et al., 1993). [The species described from southern Europe: "Habitat in Europae australis salsis."]

Annual herbs, 5–70 cm, glabrous. Stems branched from the base or nearly so, erect or ascending; branches straight or slightly arcuate (lower ones sometimes almost prostrate). Leaves (especially lower ones) mostly opposite, linear, semiterete, fleshy, in herbarium specimens usually more than 1.5 mm broad, distinctly swollen or ovate at base; apex mucronulate, non-spinose. Inflorescence spicate, distinctly interrupted. Bracts at maturity horizontally reflexed, alternate or almost opposite, abruptly narrowing into mucronulate non-spinose apex. Flowers mostly solitary in axils of bracts or reduced upper leaves. Perianth segments glabrous, with crenate to pectinate-ciliate apex, at maturity wingless or with rudimental triangular tubercles, not connate to bracteoles. Fruiting perianth ca. 3–6(7) mm diam.

Chromosome number. $2n = 18$ (Zakhar'yeva, 1985).

Habitats. Coastal and disturbed saline habitats; 0–50 m.

Distribution. Herbarium specimens were examined from California: San Mateo Co., Palo Alto Yacht Harbor near airport, altitude about sea level, 6 Oct. 1974, *J. H. Thomas 17615* (MO); Santa Clara Co., Palo Alto Yacht Harbor, near E end of yacht

basin, edge of disturbed area along salt marsh, 7 Dec. 1975, *J. H. Thomas 18062* (US). *Salsola soda* is native to Eurasia (mostly Atlantic Europe, the Mediterranean region, and southwestern Asia) and northern Africa.

Salsola soda is known from several localities in central California, near San Francisco Bay (Thomas, 1975). It can be expected to spread in California, or to appear in inland or coastal saline habitats in other southern states.

6. Salsola vermiculata L., Sp. Pl.: 223. 1753. TYPE: LINN 315.20 (lectotype, selected by Botschantzev, 1975b). [The species described from Spain: "Hispania."]

Subshrubs, 20–70(–100) cm, densely pubescent (especially when young) with smooth and minutely denticulate hairs; sometimes becoming glabrous at maturity. Stems branched at the woody base, branches erect or ascending, virgate. Leaves 5–8 × 0.5–1 mm, semiterete, usually pubescent, expanding into ovate base, bearing in their axils several reduced leaves ca. 1–4 mm long; apex obtuse. Inflorescence spicate but its primary axis sometimes paniculately branched. Bracts normally densely pubescent, obtuse. Bracteoles free. Flowers solitary or rarely 2–3 in axils of bracts or reduced upper leaves. Perianth segments sparsely pubescent above wings (especially at apex), sometimes becoming glabrous, with conical apex, winged at maturity. Fruiting perianth (including wings) 7–12 mm diam.

Chromosome number. $2n = 18$ (Sankary, 1986; the record for "*S. vermiculata* L. var. *villosa* (Del.) Moq.").

Habitats. Rocky slopes, clay soils, disturbed places; ca. 1000 m.

Distribution. Herbarium specimens were examined from California: San Luis Obispo Co., Recruit Grade Pass, 5.2 km W of Kern Co. line, Temblor Range, elev. 979 m, 3 Oct. 1978, *J. L. Johnson & G. D. Barbe 2448* (US); Temblor Range, ridge top and E slope at Crocker Grade, S of Crocker Springs Rd., ca. 2 mi. W of the county line and 7.5 mi. (airline) SW of McKittrick, elev. 3200 ft., 31 Oct. 1989, *Don Pendleton s.n.* (MO). *Salsola vermiculata* is native to the Mediterranean region.

Salsola vermiculata sensu lato is known in North America only from California, as a locally persistent escaped weed. It is naturalized near an abandoned experimental plot, Recruit Grade Pass, Temblor Range, San Luis Obispo Co. (possibly also in Kern Co.), where it was previously tested as a potential forage plant introduced from Syria in 1969. *Salsola vermiculata* is designated as a Federal Noxious Weed by the United States Department of Agriculture (Westbrooks, 1993). It is so far the only perennial species of *Salsola* sensu lato introduced to North America. Together with other related Eurasian and African taxa, it should probably be segregated into a separate genus, *Caroxylon.*

Salsola vermiculata sensu lato is a taxonomically complicated and morphologically polymorphic complex represented in Eurasia (mostly in the Mediterranean region, western and Central Asia) by several closely related races usually treated as subspecies or distinct species (Botschantzev, 1975a, b; Greuter et al., 1984). *Salsola vermiculata* sensu stricto is a western Mediterranean species occurring in southwestern Europe and northwestern Africa. Numerous records of *S. vermiculata* from Syria and other countries of the Middle East refer to other closely related species and/or subspecies, which replace it in the eastern Mediterranean region. North American material most probably belongs to *S. damascena* sensu stricto. It fits the protologue and the type specimen deposited at LE, but additional study and comparison with other Eurasian "microspecies" are necessary. Some of these taxa remain little-known and poorly understood taxonomically. Because of that I prefer provisionally to place the North American plant of Syrian origin in *S. vermiculata* sensu lato until further clarification of its taxonomic identity.

The nomenclatural citation for *Salsola damascena* and its basic synonymy are provided below.

Salsola damascena Botschantzev, Bot. Zhurn. (Leningrad) 60(4): 500. 1975. TYPE: "Syrie: Tallus pierreux du jardin Boustan el Nashé a Mezzé près de Damas, 9 Aug. 1856, *C. Gaillardot 1627*" (holotype, LE).

According to Botschantzev (1975a, b), the synonymy of *Salsola damascena* includes *S. rigida* Pallas var. *tenuifolia* Boissier (Flora Orient. 4, 2: 968. 1879, in part) and *S. vermiculata* subsp. *tenuifolia* (Boissier) Botschantzev (Novosti Sist. Vyssh. Rast. (Leningrad) 1: 375. 1964). The names *Salsola villosa* Delile (Fl. Aegypt. Illustr.: 57, No. 309. 1813, in part, excluding the type) and *S. vermiculata* subsp. *villosa* (Delile) Eig (Palest. J. Bot., ser. J, 3, 3: 132. 1945, in part, excluding the type of the basionym) were misapplied to *S. damascena* sensu stricto.

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RITMOS TEMPORALES DE LA INVESTIGACIÓN TAXONÓMICA DE PLANTAS VASCULARES EN MÉXICO Y UNA ESTIMACIÓN DEL NÚMERO DE ESPECIES CONOCIDAS[1]

Rodolfo Dirzo[2,3] *y Guillermina Gómez*[2]

Resumen

Se analizaron los patrones temporales de la investigación taxonómica en México con base en un conteo o estimación del número de taxa (específicos e infraespecíficos) descritos para ese país, a partir del establecimiento del sistema de Lineo (en 1753) y hasta 1988. Se encontraron tendencias temporales que se correlacionan con eventos históricos conocidos. El conteo acumulativo produjo un total de 23,630 nuevos taxa mexicanos descritos para la ciencia en 235 años de existencia de la taxonomía. Esta cifra se utilizó como base para estimar el número de especies conocidas de México hasta 1988 utilizando dos factores de corrección, a saber: (i) una estimación de la proporción de especies que, aunque ocurren en México, no fueron descritas para ese país, y (ii) una estimación del grado de redundancia nomenclatural (sinonimia). Con este método se llegó a un estimado total de 16,870 taxa. Además, la curva de acumulación de nuevos taxa parece que se encuentra lejos de la asíntota, y en los últimos años la tasa es mayor a 150 por año. Bajo el argumento de que aún falta por reconocer aproximadamente un 20% del total florístico del país, calculamos que el número llegaría a 20,244, cercano a la estimación de Rzedowski, de 22,800. Nuestra estimación y la de Rzedowski sugieren que la cifra ampliamente citada de 30,000 especies debe tomarse con cautela. Nuestra estimación conservadora, y la tendencia actual creciente de seguir acumulando nuevos taxa señalan a México como uno de los centros de mayor diversidad botánica del planeta.

Abstract

Temporal patterns of research on Mexican vascular plants were analyzed on the basis of counts or estimates of taxa (species and infraspecific) described from Mexico since the establishment of the Linnaean system (in 1753) up to 1988. Temporal tendencies were found that correlate with known historical events. The cumulative count yielded a total of 23,630 Mexican taxa described in the 235 years of existence of the binomial system. This number was used as a basis to estimate the number of taxa known to Mexico up to 1988 using two correction factors: (i) an estimate of the proportion of species that, even though they are present in Mexico, they were not described from that country, and (ii) an estimate of the degree of nomenclatural redundancy (synonymy). With this method we arrived at a total of 16,870 taxa. Moreover, the curve of the cumulative number of new taxa seems to be far from reaching the asymptote, and over recent years the rate is greater than 150 per year. Under the argument that approximately 20% of the total floristic richness of the country is yet unknown, we calculate that the number would rise to 20,244, close to Rzedowski's estimate of 22,800. Our estimate, and that of Rzedowski, suggests that the widely cited figure of 30,000 species should be taken with caution. Our conservative estimate and the lack of evidence of an asymptote in the rate of acumulation of taxa detected in this study underscore Mexico as one of the territories of greater floristic diversity on the planet.

La sistemática, como disciplina biológica, opera en dos principales campos de acción. El primero, comúnmente conocido como sistemática descriptiva, o taxonomía, se refiere a la exploración y recolección en el campo, conducentes al nombramiento y clasificación de los organismos. El segundo, como extensión lógica, concierne al estudio del origen, evolución y mantenimiento de la diversidad

[1] Este estudio se llevó a cabo con el apoyo económico de una beca postdoctoral de la Fundación Jessie Smith Noyes del Missouri Botanical Garden, otorgada a RD. Varios colegas del Jardín Botánico de Missouri nos ofrecieron ayuda y literatura de gran utilidad; en particular agradecemos a Roy E. Gereau, Al Gentry, Fernando Zuloaga, William D'Arcy y Dale Johnson. Jerzy Rzedowski, Peter Raven, Fernando Zuloaga y un revisor anónimo revisaron una versión preliminar y nos hicieron correcciones muy valiosas. Elizabeth Shaw nos proporcionó un listado de holótipos y lectótipos de México, a partir de las tarjetas del Gray Index, correspondientes a los últimos años.

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biológica (Raven & Johnson, 1986). De esto se desprende que la sistemática es una ciencia fundamental para muchas otras disciplinas biológicas (p. ej., ecología, fisiología, evolución), pero es además una ciencia de importancia pragmática, por ejemplo para la búsqueda e identificación de fármacos, nuevas fuentes de alimento, agentes polinizadores, agentes de control biológico, y para el diseño de unidades de conservación de la biodiversidad, etc. (Wilson, 1988a, b, c). Sin embargo, a pesar de su enorme importancia, la sistemática, aún en el primero de sus dos objetivos, todavía se encuentra lejos de cubrir su cometido. Esto es al punto tal de que, el número de especies del planeta, no se conoce siquiera en términos de su orden de magnitud. Por ejemplo, a partir de la inauguración del sistema binomial por Lineo, en 1753, se han descrito apenas unos 1.4 millones de especies, mientras que las estimaciones más recientes (p. ej., Erwin, 1983) sugieren que el número podría ser cercano a 30 millones. Claramente la sistemática, en sus dos vertientes, es un campo que requiere atención prioritaria a nivel planetario, sobre todo a la luz de las alarmantes tasas de extinción biológica contemporáneas (véase Dodson & Gentry, 1991; Raven, 1987; Sarukhán & Dirzo, 1992; Wilson, 1988c).

En esta contribución presentamos un análisis temporal de la intensidad de la investigación taxonómica de las plantas vasculares de México (exploración botánica y descripción de especies) y, como corolario, ofrecemos una estimación del posible número de especies (y taxa infraespecíficos) conocidos para el país hasta ahora. Nuestro primer objetivo se basa en un sondeo del número de taxa publicados para el país a través del tiempo. Para nuestro segundo objetivo usamos la misma base, con unas correcciones que más adelante se describen.

El territorio mexicano, de aproximadamente dos millones de km², contiene una enorme diversidad de hábitats naturales que van de la selva tropical húmeda a las comunidades de vegetación alpina; además, por su historial geológico y por su posición latitudinal, es el sitio de encuentro de floras de origen Neártico y Neotropical (véase Rzedowski, 1978, 1991) y es asiento de una de las floras más ricas del planeta (Dirzo, 1994; Rzedowski, 1978, 1991; Toledo, 1988).

Materiales y Métodos

El curso temporal de la investigación taxonómica

Para este análisis nos basamos en dos índices importantes que recopilan la información concerniente a las especies vegetales nuevas para la ciencia, el Index Kewensis (IK) y el Gray Index (GI). Ambos índices proveen los nombres de especies de plantas vasculares que se publican, incluyendo el nombre científico de la planta, el autor, el año en que se publicó la descripción de la especie, el origen geográfico y la fuente de información referente a la publicación del taxón. El GI consiste de un juego de tarjetas, cada una de las cuales contiene la información referente a un holótipo y lectótipo dado. Dicho índice se usó mayoritariamente, ya que contiene información exclusiva para las plantas del hemisferio occidental. Para nuestro análisis revisamos todas las tarjetas del GI transcritas en los volúmenes 1–12 (correspondientes a 1886–1964) (GI, 1968) y suplementos 1 y 2 (correspondientes a 1965–1977) (GI, 1978), así como las tarjetas correspondientes a los últimos 11 años (hasta 1988).

Para hacer el conteo de los taxa publicados antes de 1886, utilizamos los volúmenes 1 y 2 del IK, los cuales recopilan la información a partir del establecimiento del sistema de *Species Plantarum,* por Lineo, en 1753 (IK, 1895). Para este periodo de 1773–1885, y debido a que el IK aglutina la información para los taxa de todo el mundo, hicimos una estimación del número de especies descritas para México utilizando una muestra de 100 páginas seleccionadas al azar. Por lo tanto, para este periodo, sólo tenemos un número estimativo global del número de taxa descritos, mientras que a partir de 1886 y hasta 1988, proveemos información detallada en términos del número de taxa (obtenido por búsqueda y conteo directo) descritos por cada año.

Estimación del número de especies conocidas

El conteo de los taxa descritos de México se tomó como base para estimar el posible número de especies (incluyendo los taxa infraespecíficos). A dicho conteo se le incorporaron dos factores de corrección necesarios: (i) adición del número de especies que, aunque se distribuyen en México, no fueron descritas originalmente para ese país. Es decir, se requirió una estimación de la relación especies no descritas : especies descritas de México y después adicionar dicho estimado al conteo inicial. (ii) A esta última cifra habría que reducirla para lidiar con la redundancia de nombres (i.e., sinonimia) adjudicados a una misma entidad. En otras palabras, se requirió estimar la razón sinónimos/nombres aceptados y corregir la cifra descrita en el inciso anterior de acuerdo a ésto.

Para el primer caso se tomó una muestra al azar de nombres (600 en total) escogidos de doce floras,

flórulas o listas que aportasen la información sobre la publicación de especies. Cada nombre escogido se verificó en el IK, o en el GI, o en la publicación de su descripción original, para definir el país de origen. Las floras, flórulas o listas utilizadas fueron: Arboles y Arbustos de México (Standley, 1920–1926), Golfo de California (Johnston, 1924), Flora Novo Galiciana: Compositae (McVaugh, 1984) y Leguminosae (McVaugh, 1987); Flora Fanerogámica del Valle de México (Vol. II Dicotyledoneae) (Rzedowski & Calderón de Rzedowski, 1985); Listados Florísticos de México: IV Flora de Chiapas (Breedlove, 1986), V Angiospermas Acuáticas de México (Lot & Novelo, 1986), VI Flórula de la Isla de Cozumel (Téllez & Cabrera, 1987), VII Estación de Biología Tropical Los Tuxtlas, Veracruz (Ibarra & Sinaca, 1987); Flora de Veracruz: Chloranthaceae (Ludlow-Wiechers, 1978), Araliaceae (Sosa, 1979), Caricaceae (Moreno, 1980), Cannaceae (Jiménez, 1980), Nyctaginaceae (Fay, 1980), Clethraceae (Bárcena, 1981), Ebenaceae (Pacheco, 1981), Cyatheaceae (Riba, 1981), Papaveraceae (Martínez-Ojeda, 1982), Bignoniaceae (Gentry, 1982), Connaraceae (Forero, 1983a), Martyniaceae (Taylor, 1983), Juglandaceae (Narvae Flores, 1983), Brunelliaceae (Nee, 1985), Marattiaceae (Palacios, 1990); Flora de Chiapas: Malvaceae (Fryxell, 1990); Las Cactáceas de México (Bravo-Hollis, 1978; Bravo-Hollis & Sánchez-Mejorada, 1991).

Para el caso de la sinonimia se utilizaron nueve volúmenes de la Flora Neotropica, correspondientes a las siguientes familias (o grupos dentro de familias; ver referencias): Bignoniaceae (Gentry, 1980); Bromeliaceae (Smith & Downs, 1974, 1977, 1979); Connaraceae (Forero, 1983b); Flacourtiaceae (Sleumer, 1980); Lauraceae (Kubitzki & Renner, 1982); Lecythidaceae (Prance & Mori, 1979); Moraceae (Berg, 1972); Olacaceae (Sleumer, 1984); Zingiberaceae (Maas, 1977). Una ventaja de la Flora Neotropica es que se incluyen todos los sinónimos existentes para cada nombre, no sólo los sinónimos conocidos a nivel local (como en el caso de otras floras regionales más específicas para México). De estas floras se escogieron nombres al azar (380 en total) y a cada uno de ellos se les contó el número de sinónimos. Además, se utilizó el análisis de los sinónimos correspondientes a las Solanaceae, a nivel mundial, derivado del tratamiento reciente de la familia por D'Arcy (1990, y com. pers.). Con las razones sinónimos/nombres aceptados calculadas para cada grupo, se calculó una razón promedio, la cual fue utilizada como factor de corrección de la redundancia nomenclatural.

Resultados y Discusión

La investigación taxonómica a través del tiempo

El muestreo aleatorio de los volúmenes I y II de IK (que abarcan de 1753 a 1885) arrojó un promedio de 3.07 (error estándar ± 0.759) especies descritas para México, por página de dicho índice. El total de páginas (considerando sólo aquellas que contienen listados de especies) que incluyen estos volúmenes es igual a 2525 [i.e., 1268 (Vol. I) + 1257 (Vol. II)]. Por lo tanto, con base en el promedio, el número estimado de especies para ese periodo es $3.07 \times 2525 = 7752$. Un conteo directo de las primeras 100 páginas del Vol. I arrojó un valor de 310 especies; este número es considerablemente cercano al valor de 307 que se estimaría con base en el muestreo aleatorio. Adicionalmente, dado que el IK no contiene información referente a taxa infraespecíficos, éstos se contaron directamente del GI, el cual sí provee la información (a partir de 1753) para dichos taxa. El total de nombres infraespecíficos contados fue 480, el cual sumado al valor de 7752, produce un total de 8232 para el periodo que va de Lineo hasta 1885. Este resultado implica, crudamente, que para este lapso inicial del estudio taxonómico de las plantas vasculares de México, la tasa de "descubrimiento" y descripción de plantas nuevas para la ciencia era de 58 por año.

A partir de 1886, el conteo directo del GI nos permite ofrecer una imagen más detallada del curso temporal del estudio taxonómico para las plantas vasculares de México (Fig. 1). Para el resto del siglo XIX la tasa de descripción de especies (mas los taxa infraespecíficos) procedió a un ritmo (promedio) notablemente alto, 250 por año, observándose las máximas oscilaciones en 1892 (79 especies) y 1894 (481 especies). La existencia de los altos valores iniciales es explicable por la extraordinaria y tesonera labor de algunos botánicos, entre los que sobresalen el Español Martín Sessé y el Mexicano José Mariano Mociño, en particular por sus monumentales obras (en coautoría) Plantae Nova Hispaniae (1887–1891) y Flora Mexicana (1887–1897), aunque muchos de los taxa nombrados deben ser sinónimos. (Para una discusión de las posibles fechas correctas de la publicación original de estas obras en La Naturaleza, véase Smith, 1942.) El tercio final de este siglo es seguido por otro lapso que, bajo el nuestro sensor de nuevos taxa descritos, parece ir en caída, sobre todo a partir de 1910 (coincidiendo con la Revolución Mexicana) y por una década subsecuente. Este lapso de 1900 a 1920 acusa un promedio de nuevos taxa por año de 170, e incluye el segundo valor indi-

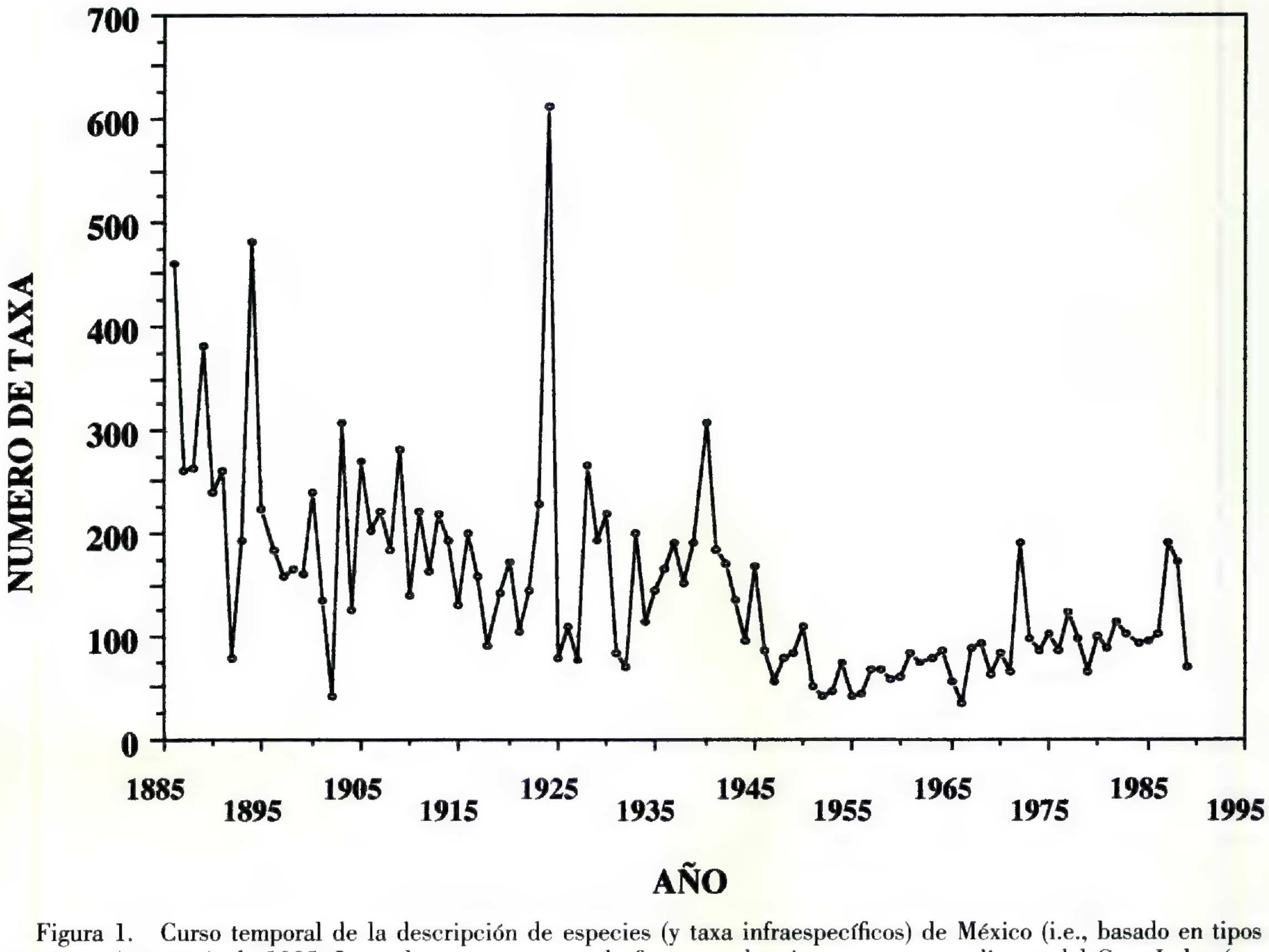

Figura 1. Curso temporal de la descripción de especies (y taxa infraespecíficos) de México (i.e., basado en tipos mexicanos), a partir de 1885. Los valores que muestra la figura se obtuvieron por conteo directo del Gray Index (ver detalles en el texto).

vidual anual más bajo (44) de todos los tiempos. El periodo de 1920 a 1950 es de cierta recuperación pero, más notablemente, de marcada oscilación, registrándose aquí el mayor valor anual de taxa de toda la historia, en 1924 (612). En este periodo que Rzedowski (1981: 10), llama la "etapa heroica de la botánica mexicana" destacan las contribuciones de Mexicanos excepcionales como Maximino Martínez, en conjunción con las obras monumentales de algunos extranjeros como Trelease (1924) con sus estudios sobre *Quercus* y la excepcional antología sobre los árboles y arbustos de México de Standley (publicada en el lapso de 1920–1926). Estas contribuyen de manera significativa a la proliferación taxonómica observada y explican en buena medida el inusitado pico de 1924. El periodo de 1951 a 1970 observa una disminución sensible, con un promedio de 70 taxa nuevos por año, y con menos oscilación. En este intervalo calificado por Rzedowski (1981: 12) como "la etapa de estudios sobre la vegetación" las contribuciones taxonómicas son mayoritariamente de extranjeros.

Finalmente, en las últimas dos décadas, se nota una resurgencia de la investigación taxonómica, con una notable contribución de botánicos Mexicanos (complementaria a la aún mayoritaria contribución de taxonómos extranjeros) y con un impresionante promedio anual de 110 taxa. Es de destacar que en este periodo reciente, han surgido hallazgos inusitados como el descubrimiento de una excepcional familia, Lacandoniaceae (Orden Triuridales), con características morfológicas sorprendentes (véase Márquez-Guzmán et al., 1989; Martínez y Ramos, 1989), así como el revolucionario descubrimiento del maíz diploide, perenne (Iltis et al., 1979).

ESTIMACIÓN DEL NÚMERO DE ESPECIES (Y TAXA INFRAESPECÍFICOS)

Con los datos del número de taxa descritos para cada año (cf. Fig. 1), se elaboró una curva del número acumulativo de especies (incluyendo los taxa infraespecíficos) a través del tiempo (Fig. 2). Por simplicidad, los puntos de la curva corresponden al valor sumado de cinco años consecutivos. De hecho, en los últimos 100 años (1888–1988) se describió el doble de especies (15,398) del número descrito en el periodo correspondiente al lapso que va desde la implantación del sistema de Lineo (en

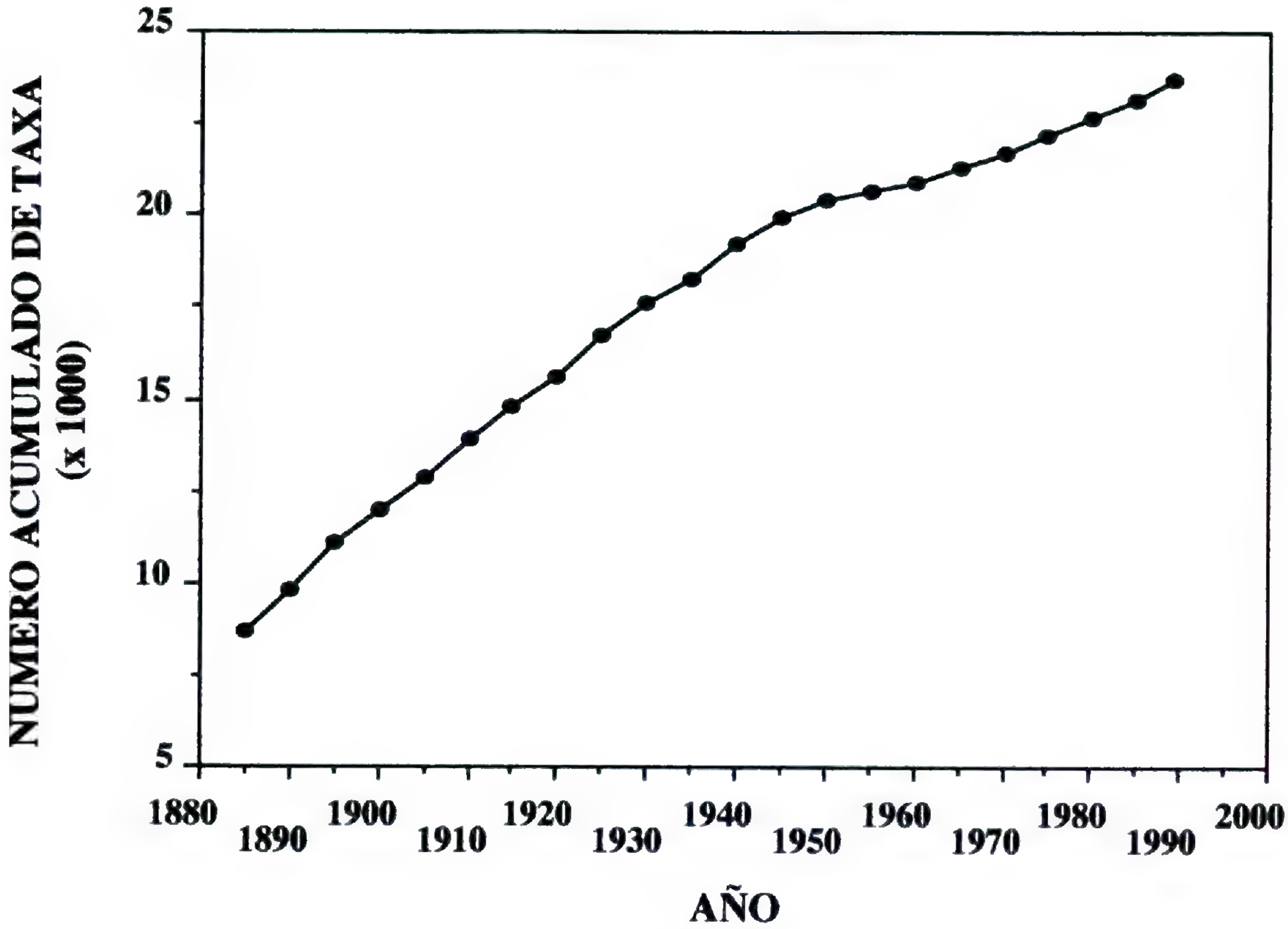

Figura 2. Número acumulado de taxa descritos para México, a través del tiempo. Cada punto en la curva corresponde al valor sumado de taxa en periodos subsecuentes de cinco años. El valor acumulado correspondiente a 1885 se obtuvo a partir del muestreo del Index Kewensis (ver detalles en el texto).

1753) hasta la iniciación del GI (1886). A partir de la curva acumulativa se llega a un total de 23,630 taxa nombrados formalmente hasta 1988, aunque es evidente que la curva aún no muestra una asintotización.

Nuestro número final estimado de 23,630 tiene los siguientes atributos: (i) no toma en cuenta que la flora del país incluye especies descritas en otros países (es decir, no basadas en tipos de México), y (ii) no considera la redundancia de nombres adjudicados a una misma entidad específica. La depuración de estas dos características nos permitiría ofrecer una estimación del número de especies conocidas de México.

La corrección referente a la relación especies descritas: no descritas para México se basa en los resultados del Cuadro 1 (ver Materiales y Métodos). Las doce floras, flórulas o listas analizadas varían en la proporción de taxa descritos para México desde 20 (Cozumel) a 84.2% (Compositae de Nueva Galicia). Dado que la proporción global calculada es influenciable por el tamaño de muestra utilizado para el cálculo de la relación de cada flora en particular (por ejemplo, si una relación baja es resultante de un tamaño de muestra grande, la relación global tenderá a ser desproporcionadamente baja) se tomó, como criterio conservador, el promedio de las doce relaciones individuales. Con este criterio, la proporción resultante es 46.86% "mexicanas": 53.14% "no mexicanas." Aplicando este promedio de 46.86% como factor de corrección a nuestro valor de 23,630, el número que se obtiene pasa a 50,427 (i.e., 23,630 × 100/46.86).

Nuestro factor de corrección tiene un coeficiente de variación de 40.6%, lo cual resulta en parte adjudicable al tamaño de muestra (N = 12 floras/flórulas/listas). Desafortunadamente no parece existir otra fuente de información disponible con la cual confrontar nuestra proporción. Debido a su interés intrínseco y su potencial de aplicación, sería de gran utilidad calcular la proporción en cuestión con un tamaño de muestra más robusto.

Finalmente, nuestra corrección referente a la redundancia nomenclatural (sinonimia) se basa en los resultados del Cuadro 2. La razón sinónimos: nombres válidos varió considerablemente entre grupos, con un ámbito de 0.62 (Connaraceae) a 4.37 (Flacourtiaceae). Nuevamente, por las razones expuestas para la corrección anterior, se optó por el criterio más conservador de utilizar el valor promedio, el cual resultó de 1.989 (coeficiente de variación = 56.2%). Con base en esta muestra calculamos que por cada nombre hay casi dos sinónimos. Aplicando este factor de corrección se llega, finalmente, a un estimado de 16,870 (i.e., 50,427/2.989) es-

Cuadro 1. Cálculos del número de especies descritas de México y de otros países, obtenidos del muestreo de doce floras, flórulas o listas. Estos datos se utilizaron para estimar el porcentaje de especies descritas con respecto a las no descritas de México, pero que se distribuyen en el mismo país. ($\bar{x}$ = promedio de los doce porcentajes; D.E. = desviación estándar.)

Flora/flórula o listado*	Descritas de México	Descritas de otros países	Total	%
Cactáceas de México	33	15	48	68.75
Arboles y arbustos	70	29	99	70.70
Chiapas	14	30	44	31.82
Chiapas: Malvaceae	8	13	21	38.10
Acuáticas	4	14	18	22.22
Cozumel	2	8	10	20.00
Flora de Veracruz	13	22	35	37.14
Los Tuxtlas	6	14	20	30.00
Golfo de California	27	29	56	46.43
Nueva Galicia: Legum.	50	47	97	51.55
Nueva Galicia: Comp.	80	15	95	84.21
Valle de México: Dicot.	34	23	57	59.65
$\bar{x}$ ± D.E.				46.86 ± 19.04

* Las referencias para estas fuentes de información se dan en la sección de Materiales y Métodos.

pecies y taxa infraespecíficos conocidos hasta 1988 para el territorio mexicano.

La tendencia temporal mostrada en la Figura 2 señala claramente la ausencia de un patrón asintótico hacia el final del lapso computado. De hecho, en los dos últimos años (1987 y 1988) para los que se recopiló la información completa del IG, nuestra búsqueda arrojó valores de 191 y 173 taxa, respectivamente. Es decir, la proyección inmediata es que, de seguir la misma tendencia, los próximos años verían una tasa mínima subsecuente de más de 150 especies por año (tal vez el número sería más cercano a 200 que a 150). Desde luego, es esperable una asintotización de la curva, pero resulta claro que la flora mexicana aún tiene un potencial de incremento. Rzedowski (1991) argumenta que el porcentaje de las especies de fanerógamas reconocidas está por debajo del 90% del total, aunque seguramente por encima del 75%, y estima que "un complemento de 20% . . . tal vez constituya una aproximación razonable" (p. 6). Si agregamos dicho complemento a nuestra estimación de 16,870, se llega a un total de 20,244. Este valor se acerca a la predicción preliminar de Rzedowski (1978: 73) de que la flora mexicana podría sobrepasar el valor de 20,000, así como a su predicción más reciente de 22,000 especies (Rzedowski, 1991). La información disponible, aún parcial, para el año de 1989, agrega ya otras 100 especies nuevas para la ciencia, y la tendencia inmediata extra-

Cuadro 2. Estimación de la relación entre el número de sinónimos y el número de nombres válidos con base en el análisis de diez familias (o grupos dentro de familias) de plantas.

Familia*	Sinónimos (A)	Nombres válidos (B)	Razón (A/B)
Bignoniaceae	38	26	1.462
Bromeliaceae	198	150	1.320
Connaraceae	31	50	0.620
Flacourtiaceae	131	30	4.367
Lauraceae	32	15	2.133
Lecythidaceae	46	25	1.840
Moraceae	54	40	1.350
Olacaceae	30	24	1.250
Solanaceae	7793	2297	3.393
Zingiberaceae	43	20	2.150
$\bar{x}$ ± D.E.			1.989 ± 1.118

* Las referencias para esta fuentes de informacíon se dan en la sección de Materiales y Métodos.

polable de nuestro sondeo (cf. Figs. 1 y 2) hace pensar que, efectivamente, el número sobrepasará las 20,000 especies. Sin embargo, nuestra estimación es considerablemente menor a la proyección hecha por Toledo (1988: 17) de que la flora mexicana "se estima en 30,000 especies de plantas vasculares," es decir, un 36 y un 48% adicional a las estimaciones mínimas 22,000 de Rzedowski (1991) y de 20,244 de este estudio, respectivamente. Aunque la tendencia del número de especies por describirse va en aumento (cf. Fig. 2), claramente, el grado de redundancia nomenclatural debe tomarse en consideración para tales proyecciones.

Una observación de nuestros resultados del Cuadro 2 revela que cualquier modificación del factor de corrección de la sinonimia, aun cuando pequeña, puede alterar marcadamente el número estimado. Es necesario enfatizar que nuestros resultados son totalmente dependientes de las fuentes de información nomenclatural la cual, al momento, dista de ser óptima o es limitada. Aún tomando en cuenta estas salvedades, es claro que la riqueza florística del territorio mexicano es notable y sobrepasa las expectativas iniciales (véase revisión de Rzedowski, 1978: 73) y sobrepasa la de otros países de mayor extensión como los Estados Unidos de Norteamérica, Canadá o la ex-Unión Soviética (Rzedowski, 1991). La India, con una extensión mayor que México (3.3 vs. 2.0 millones km^2) con una posición latitudinal similar, con gran variedad de ambientes (selvas a vegetación alpina), y para la cual existe una enumeración floristica reciente, suma tan sólo 15,000 (S. K. Jain, com. pers. 1990). Toledo (1988) cita otras comparaciones que igualmente subrayan la enorme riqueza florística de México.

La definición de la magnitud de la diversidad botánica de una región y finalmente del planeta, es de gran importancia académica y aplicativa (Wilson, 1988a, b, c). En el caso de México, la estimación de unas 17,000 especies nombradas hasta 1988 y la tendencia creciente señalada, sugieren que la flora de este territorio bien podría acercarse a contribuir con ca. 7% de la flora total del planeta (i.e., considerando que hasta ahora se han descrito un poco menos de 250,000 especies de plantas (Wilson, 1988a)). Desde luego, contra este notable potencial de contribución florística a nivel planetario, habrá que contraponer la tremenda alteración de los hábitats y potencial de extinción de plantas en México (véase, por ejemplo, Dirzo & García, 1990; Flores-Villela & Geréz, 1988; Rzedowski & Calderón de Rzedowski, 1987). Una vez más, este estudio hace resaltar lo obvio: la investigación taxonómica es de importancia medular y aún tiene mucho por hacer pero, además, es éste un quehacer científico en clara carrera contra el acelerado reloj de la deforestación y la extinción biológica.

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DIVERSITY OF THE FLORA OF FAN SI PAN, THE HIGHEST MOUNTAIN IN VIETNAM[1]

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ABSTRACT

Fan si Pan, situated in northern Vietnam near the border with China and reaching an altitude of 3143 m, is the highest mountain in Vietnam. The flora of this mountain and surrounding region is rich, containing a mixture of subtropical and temperate components. It also supports many relictual plant species that possibly represent remnant extensions of the old, subtropical flora of the southern Yunnan Province of China. The flora is diverse and characterized by the following: Aceraceae (*Acer*); Cupressaceae (*Fokienia hodginsii* (Dumm) Henry & Thomas); Ericaceae (*Rhododendron, Vaccinium*); Fagaceae (*Castanea, Castanopsis, Fagus, Lithocarpus, Quercus*); Juglandaceae (*Carya, Engelhardia, Juglans, Platycarya*); Lauraceae (*Beilschmiedia, Machilus, Phoebe, Neolitsea*); Magnoliaceae (*Liriodendron, Magnolia, Manglietia, Michelia*); and Pinaceae (*Abies nukiangensis* Cheng & L. K. Fu, *Tsuga chinensis* (Franch.) Pritz).

Fan si Pan, located at 22°09′–23°30′S, 103°–103°59′E and reaching an altitude of 3143 m, is the highest point in Vietnam. It is situated in the mountainous northwest province of Láo Cai. Fan si Pan and its contiguous mountain range are oriented along the Red River in roughly a northwest to southeast direction and extend into the Yunnan Province of China and to the Himalayan chain to the northwest. This range of mountains is derived from rocks of gneiss and ancient granite. The climate is humid or perhumid (76–96%) year-round with an average yearly rainfall of 2770 mm; the heaviest rains are concentrated in the months of July and August. The average temperature is about 15°C, with a range between −3°C and 20°C. December and January are the coldest months, when snow can fall for 1–3 days each year.

This paper presents a listing of plant species from this diverse region of Vietnam, discusses the main vegetation types occurring there, and relates the Sino-Himalayan affinities of specific taxa to past climatic shifts believed to have occurred in this region.

FLORISTIC DIVERSITY

On the basis of published works by Lecomte (1907–1951), Vo Van Chi (1975), Aubreville et al. (1960–1983), Ke et al. (1969–1976), Ho (1970–1972, 1991–1993) and Loc (1984), and results from our preliminary investigations (1991–1992), the flora of Fan si Pan is reported and arranged according to the Brummitt (1992) system, including 1750 species belonging to 680 genera in 210 families of 7 divisions as presented in Table 1.

Table 2 shows that in only 22 families, 746 species, or 43% of the total species found on Fan si Pan, are represented. There are several widespread and well-known families with abundant taxa represented in the flora. The most significant of these include the Orchidaceae (26 genera and 62 species), Asteraceae (36 genera and 59 species), Ericaceae (6 genera and 58 species), Poaceae (30 genera and 47 species), and Cyperaceae (6 genera and 42 species).

In the Fan si Pan flora there are also many species-rich genera with a large number of taxa. These genera are listed in Table 3.

Table 3 shows that in only 26 genera, representing 3.8% of the 680 known genera in the region, the 388 species comprise nearly 22% of the total in the flora, suggesting that the region around Fan si Pan and the local conditions have selectively encouraged diversification in several genera.

A diversity of morphologies are found in the flora

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Table 1. Diversity of plant divisions represented in the flora of Fan si Pan.

Division	Species	Genera	Families
Bryophyta	180	40	25
Psilotophyta	1	1	1
Lycopodiophyta	20	2	2
Equisetophyta	2	1	1
Polypodiophyta	300	86	27
Gymnospermae	10	8	6
Angiospermae	1237	542	148
Dicotyledons	1022	443	131
Monocotyledons	215	99	17
Totals	1750	680	210

as well. Widespread forest genera with large trunks are found, such as *Beilschmiedia, Phoebe, Machilus* (Lauraceae); *Eberhardtia* (Sapotaceae); *Castanopsis, Lithocarpus* (Fagaceae); *Schima* (Theaceae); *Altingia* (Hamamelidaceae); and *Fokienia* (Cupressaceae). Different from typical tropical trees from hot, humid forest conditions, species of these woody plants from Fan si Pan lack buttresses. Woody lianas are for the most part absent from the flora, yet vines are common.

Besides mosses, which are very common, the most common epiphytes found in the Fan si Pan flora are in the following families: Acanthaceae: *Staurogyne petelotii* R. Ben.; Ericaceae: including *Rhododendron poilanei* Dop, *Vaccinium poilanei* Dop; Gesneriaceae: *Lysionotus petelotii* Pell., *Lysionotus* spp., and *Aeschinanthus*; Loranthaceae: *Loranthus parasiticus* Druce; Orchidaceae: *Liparis* spp., *Dendrobium* spp., and *Aerides* spp. Distinctive from other typically tropical and subtropical floras are epiphytic species in the Ericaceae, Acanthaceae, and Gesneriaceae.

The herbaceous plant composition varies with microclimatic conditions, and thus with habitat. Along streams or in moist valleys under the cool, shaded forest canopy there are several species of Acanthaceae, Aristolochiaceae, Begoniaceae, Gesneriaceae, Myrsinaceae, Piperaceae, and Urticaceae. Under the dense forest canopy in deep shade the few plants that can survive are those that do not depend on light for growth but, rather, obtain nutrients from decaying plant matter, such as the saprophytic *Balanophora pierrei* Van Tiegh. It is worth noting here that taxa of Aristolochiaceae, Begoniaceae, Gesneriaceae, and Urticaceae are very

Table 2. Most species-rich families in the flora of Fan si Pan ranked by species.

Family	Genera	Species
Rosaceae	12	80
Orchidaceae	26	62
Asteraceae	36	59
Ericaceae	6	58
Poaceae	30	47
Cyperaceae	6	42
Lamiaceae	23	42
Rubiaceae	12	38
Urticaceae	10	37
Fagaceae	5	33
Moraceae	4	28
Theaceae	10	27
Gesneriaceae	11	23
Myrsinaceae	4	23
Fabaceae	10	21
Lauraceae	8	21
Acanthaceae	9	20
Commelinaceae	10	20
Aceraceae	1	19
Symplocaceae	1	16
Magnoliaceae	4	15
Melastomataceae	10	15
Totals	248	746

Table 3. Most speciose genera in the flora of Fan si Pan ranked by total number of species.

Genus	Family	Number of species
Rhododendron	Ericaceae	40
Rubus	Rosaeae	36
Carex	Cyperaceae	36
Ficus	Moraceae	23
Acer	Aceraceae	19
Symplocos	Symplocaceae	16
Asplenium	Aspleniaceae	15
Diplazium	Woodiaceae	15
Lithocarpus	Fagaceae	13
Liparis	Orchidaceae	12
Vaccinium	Ericaceae	12
Viola	Violaceae	12
Castanopsis	Fagaceae	11
Eurya	Theaceae	11
Pilea	Piperaceae	11
Ardisia	Myrsinaceae	10
Begonia	Begoniaceae	10
Dryopteris	Dryopteridaceae	10
Lepisorus	Polypodiaceae	10
Meliosma	Sabiaceae	10
Polygonum	Polygonaceae	10
Pteris	Adiantaceae	10
Michelia	Magnoliaceae	9
Clematis	Ranunculaceae	9
Quercus	Fagaceae	9
Tetrastigma	Vitaceae	9
Total		388

common in the flora of Fan si Pan, while some families that could be expected here because they are common in many other tropical forests are mostly absent, such as taxa in the Araceae and Euphorbiaceae.

A great number of species occur at Fan si Pan that have attractive flowers and leaves or interesting leaf shapes, particularly species of Ericaceae: *Rhododendron* (40 species), with various-colored flowers; Aceraceae: *Acer* (19 species); Hippocastanaceae: *Aesculus wangii* Hu; Rosaceae: *Sorbus*, with leaves becoming red in winter; Trilliaceae: *Paris* (3 species), with attractive flowers and leaves. Many of these species could be valuable to horticulture as subtropical and temperate ornamentals.

Diversity of Floristic Components

The flora of Fan si Pan is also interesting for its apparently high endemism. Preliminary estimates from the available information accumulated for this study indicate that up to 30% endemism occurs in the flora. For example, the Orchidaceae have 19 endemic species reported for northern Vietnam; 18 of them can be found at Fan si Pan. The genus *Carex* of the Cyperaceae has 7 species endemic to northern Vietnam; 6 of these have been collected at Fan si Pan. According to Vo Van Chi (1975), 25 genera and 39 species were discovered and initially described from collection records from Fan si Pan.

The Fan si Pan flora supports tropical, subtropical, and temperate elements.

TROPICAL ELEMENT

Most of the tropical elements in the Fan si Pan flora are distributed well below an altitude of 1500 m, yet some extend as high as 2000 m. These taxa are members of the Annonaceae, Araceae, Clusiaceae, Combretaceae, Cyatheaceae, woody Euphorbiaceae, Gnetaceae, Hernandiaceae, Icacinaceae, Polygonaceae, and Proteaceae. Such tropical genera and species as *Actinodaphne*, *Aleurites*, *Artocarpus*, *Calamus*, *Caryota*, *Citrus*, *Duabanga*, and *Wendlandia* are relatively common elements of the flora and constitute a significant component of the forest. This is true not only of the forest trees but also of the tropical understory shrubs and herbs that are common, such as species of *Acorus*, *Anotis*, *Balanophora*, *Calamus*, *Dichroa*, *Dioscorea*, *Diospyros*, *Disporum*, *Macaranga*, *Mallotus*, *Pasania*, *Sarcandra*, *Vernicia*, and *Wendlandia*.

SUBTROPICAL ELEMENT

The subtropical component of the flora of Fan si Pan possibly represents a Tertiary floristic element from North Vietnam–South China suggested by the following families: Aceraceae (*Acer* with 19 spp.), Cyperaceae (*Carex* with 36 spp.), Fagaceae, Gesneriaceae, Hamamelidaceae, Lauraceae, Magnoliaceae, Myrsinaceae, Symplocaceae (*Symplocos* with 16 spp.), Theaceae, and Urticaceae. Most of the subtropical species found at Fan si Pan are located near 1600 m elevation, which is characterized by an average temperature of 15.7°C and nearly 2732–2778 mm of precipitation per year. Characteristics of the elevation, climate, and geomorphology of this region combine to maintain this subtropical element of the flora.

Subtropical taxa are represented by the following genera and species: *Hydrangea* (Hydrangeaceae); *Embelia* (Myrsinaceae); *Polygonum capitatum* F. Ham. ex D. Don, *P. flaccidum* (Meissn.) Steud., *P. palmatum* Dunn, *P. thunbergii* Sieb. & Zucc. (Polygonaceae); *Anemone* (Ranunculaceae); *Huodendron*, *Rehderodendron* (Styracaceae); *Crawfurdia*, *Gentiana* (Gentianaceae); *Schisandra*, *Kadsura* (Schisandraceae); *Buddleja*, *Fagraea* (Loganiaceae); *Cornus* (Cornaceae); *Allomorpha*, *Anerincleistus*, *Bredia*, *Fordiophyton*, *Oxyspora*, *Plagiopetalum*, *Sarcopyramis* (Melastomataceae); *Viola* (Violaceae); *Adinandra*, *Anneslea*, *Gordonia*, *Pyrenaria* (Theaceae); *Exbucklandia*, *Rhodoleia* (Hamamelidaceae); *Liriodendron*, *Manglietia*, *Magnolia* (Magnoliaceae); and *Sorbus*, *Potentilla* (Rosaceae).

TEMPERATE ELEMENT

At altitudes above 2000 m, the Fan si Pan flora contains temperate floristic elements characterized by *Paris* (Trilliaceae); *Alnus*, *Betula* (Betulaceae); *Enkyanthus*, *Leucothoea*, *Pieris*, *Rhododendron*, *Vaccinium* (Ericaceae); *Celtis*, *Ulmus* (Ulmaceae); *Castanea*, *Fagus*, deciduous *Quercus* (Fagaceae); *Aesculus* (Hippocastanaceae); *Juglans*, *Platycarya* (Juglandaceae); *Crawfurdia*, *Gentiana* (Gentianaceae); *Abies*, *Tsuga* (Gymnospermae); *Huperzia* spp. (Lycopodiophyta); *Coptis*, *Ranunculus* (Ranunculaceae); *Panax* (Araliaceae); *Hypericum* (Clusiaceae); *Salix* (Salicaceae). These genera are speciose, and many are quite frequent and widespread in this region, including, in particular, *Rhododendron* with 40 species, *Vaccinium* with 12, and *Quercus* with 9.

Diversity of Vegetation Types

Although the diversity of vegetation types occurring at Fan si Pan is not yet fully understood, we can preliminarily report on the main types encountered. Their distributions appear to be associated with elevation.

1. TROPICAL VEGETATION BELT

The tropical vegetation belt formerly contained forest vegetation that has mostly been destroyed by shifting cultivation, overexploitation, and forest fires. It has subsequently been replaced by secondary forest along the valleys and by savanna on the slopes in areas not converted to cassava, rice, or maize cultivation.

1.1. Secondary forest type. This derived vegetation type is extensive and distributed along the many river and stream valleys. It is characterized by species of Lauraceae, Fagaceae, Meliaceae, Sapindaceae, Fabaceae (including Mimosaceae and Caesalpiniaceae), Magnoliaceae, and Burseraceae.

1.2. Savanna. The savanna vegetation type is also extensive and is derived spontaneously after cultivation is abandoned in a shifting agricultural system. It is characterized by the grasses *Miscanthus floridulus* (Labill.) Warb. ex K. Schumann & Lauterb. and *Saccharum arundinaceum* Retz., with some invasive and widespread trees; *Mallotus paniculatus* (Lam.) Muell.Arg., *Macaranga denticulata* Muell. Arg., *Trema orientalis* (L.) Blume, with *Musa* spp. in wetter places, and *Imperata cylindrica* (L.) Raeusch., *Cratoxylon polyanthum* Korth., *Rhodomyrtus tomentosa* (Aiton) Hassk., and *Melastoma candidum* D. Don in drier places.

2. SUBTROPICAL VEGETATION BELT

This subtropical zone can be delimited roughly between 1000 and 2000 m elevation. The temperature between these altitudes is extremely stable with a range between 15° and 17°C. Many of the subtropical taxa occurring in this zone have affinities with the Tertiary flora of northern Vietnam and southern China.

2.1. Dense evergreen forest. Dense evergreen forest was once widespread in this zone; however, due to extensive overexploitation and shifting cultivation, it can now be found only in isolated and inaccessible steep valleys and on steep slopes. The characteristic families of the forest trees are representatives of the Betulaceae, Fagaceae, Hamamelidaceae, Lauraceae, Magnoliaceae, Sapotaceae, and Theaceae.

2.2. Subtropical savanna. The derived subtropical savanna is a common type of vegetation found at these altitudes at present. It is secondary, arising after the destruction of subtropical forest most commonly by overexploitation or shifting cultivation. This widespread vegetation type is characterized by herbaceous species such as the grasses *Arundinella nepalensis* Trin., *Imperata cylindrica*, *Microstegium* sp., and *Miscanthus floridulus*; shrub species including *Buddleja* spp., *Clematis leschenaultiana* DC., *Litsea cubeba* (Lour.) Pers., *Luculia intermedia* Hutchinson, *Osbeckia crinita* Benth., *Oxyspora paniculata* (D. Don) DC., *Polygonum chinense* L. var. *scabrum*, *P. paniculatum* Andrz., *Porana racemosa* Roxb., *Rubus ellipticus* Smith, and *Viburnum cylindricum* Buch.-Ham. ex Don; and some trees, including *Acer campbellii* Hook. & Thoms. ex Hiern., *Alnus nepalensis* D. Don, *Itoa orientalis* Hemsl., *Platycarya kwangtungensis* Chun, *Sauravia nepalensis* DC., and *Wightia speciosissima* (D. Don) Merrill.

2.3. Subtropical grassland. Subtropical grassland is also derived after shifting cultivation, trampling and grazing by cow-buffaloes, and forest fire. Species of Poaceae, Cyperaceae, Fabaceae, and *Pteridium*, and including several shrubby species of *Melastoma*, *Osbeckia*, *Rubus*, and *Artemisia*, predominate.

3. TEMPERATE VEGETATION BELT

Temperate vegetation is found at altitudes over 2000 m and supports temperate species indicated by species in such genera as *Abies*, *Acer*, *Adinandra*, *Aesculus*, *Agapetes*, *Alnus*, *Altingia*, *Coptis*, *Cornus*, *Crawfurdia*, *Embelia*, *Enkyanthus*, *Fagus*, *Fokienia*, *Hydrangea*, *Huodendron*, *Liriodendron*, *Magnolia*, *Oxyspora*, *Primula*, *Quercus*, *Rehderodendron*, *Rhododendron*, *Rhoiptelea*, *Sorbus*, *Ternstroemia*, *Vaccinium*, and *Valeriana*, among others.

3.1. Temperate forest. Temperate forest vegetation composed of the above-mentioned genera is found in the deep valleys and on steep slopes of Fan si Pan. In general, this vegetation is relatively widespread at high altitudes, where it is dominated by species in the Aceraceae, Hippocastanaceae, Fagaceae, Magnoliaceae, Lauraceae, Cupressaceae, Podocarpaceae, Pinaceae, and Taxaceae.

3.2. Montane cold savanna. This very localized vegetation type occurs on the slopes of the highest summits of Fan si Pan, which are believed to have been originally covered by forest. Again, conversion of the original forest to its present vegetation type was a result of human cultivation and burning of these areas. The montane, cold savanna supports many species of shrubs and herbaceous species belonging to the Poaceae, Cyperaceae, Liliaceae, Hypoxidaceae, Zingiberaceae, Gentianaceae, Ericaceae, Rosaceae, Melastomataceae, Lamiaceae, Hypericaceae, Gesneriaceae, and Pteridophyta.

These species are light-loving and cold-enduring, with *Arundinaria* spp. as dominant.

Archaic Character of the Fan si Pan Flora

Fan si Pan contains an archaic element in the flora represented by the number of monotypic families or endemic genera that are present in the region. Families such as Bretschnederaceae, Pentaphyllacaceae, Rhoipteleaceae, and Sargentodoxaceae are present at Fan si Pan. The high level of endemism, particularly for the genera and species in the Orchidaceae, and diversity in the genus *Carex*, also support the contention that this region represents a refugium for these limited distribution taxa.

Many relictual species in the genera *Exbucklandia, Fokienia, Rhodoleia, Rhoiptelea,* and *Sargentodoxa* (Wu Cheng Yi, 1965) occur in this region. These genera represent extensions of floristic elements from a more northern flora, particularly the subtropical flora of southern China and adjacent areas, and suggest that the more tropical climate existed across this area in the past. Fan si Pan appears to have served as a protected area for many of these taxa during glacial extensions across this region. Because of the high diversity in the flora, this has long been recognized as a center for angiosperm radiation (Takhtajan, 1969). The interaction of climate, geomorphological features (including soil), and geology has supported an enrichment of the flora. Archaic characters of the geological structure of Vietnam support the presence of primitive vegetation and a high number of relictual species, which have occurred there for a long time and still survive today (Thai Van Trung, 1978).

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TOWARD AN IMPROVED CLASSIFICATION OF LAURACEAE[1]

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Abstract

Published suprageneric classifications of Lauraceae and the characters used in these classifications are briefly reviewed. It is concluded that androecial characters such as number of stamens and number of anther cells are often variable even within genera and that these characters should not be used in a classification of Lauraceae. As a first step toward an improved classification, Lauraceae are divided into two subfamilies, one consisting of *Cassytha*, the other including all other genera. The latter group is divided into three tribes, the Laureae, Perseeae, and Cryptocaryeae, based on characters of wood and bark anatomy and inflorescence structure.

Lauraceae form a large, predominantly tropical family of trees and shrubs, with the exception of *Cassytha*, an herbaceous parasite. The family is best represented in the American and Asian tropics, and has also a rather large number of species in Australia and Madagascar, but is poorly represented in Africa. About 50 genera are currently recognized, with 2500–3000 species.

Economically, Lauraceae are an important group. Many species yield high-quality timber, others spices or aromatic oils, and *Persea americana* Miller is cultivated worldwide for its edible fruits.

Ecologically, Lauraceae are, in the New World, a very important group. They are present in wet forest at any elevation (from sea level to *páramos*) and are frequently the most common or one of the most common tree families, especially in the foothills and at middle elevations of the Andes.

In spite of their importance, Lauraceae are, in respect to classification and species numbers, poorly known. Our lack of knowledge of species numbers and distribution is no doubt related to the fact that many species are tall trees with small, inconspicuous flowers, difficult to locate and to collect. This is clearly shown by a recent floristic treatment (Australia: 115 species, of which 46 were new, Hyland, 1989), recent revisions (*Nectandra:* 114 species, of which 33 were new, Rohwer, 1993a; *Pleurothyrium:* 40 species, of which 20 were new, van der Werff, 1993), and the fact that in the most recent monograph of *Aniba* (Kubitzki, 1982) not a single collection was recorded from Ecuador, while currently 11 species are known from that country. More intensive collecting will hopefully correct this lack of knowledge.

Lauraceae have, with a few exceptions, trimerous flowers. Flowers are bisexual or unisexual. There are two whorls of three tepals; the whorls are usually equal in size and shape, but in some cases the whorls are unequal. If the whorls are unequal, the outer whorl is usually smaller than the inner one, although the reverse can also be the case. Flowers have four whorls of three stamens, but in most genera, one, two, or three whorls are reduced to staminodia. The anthers open by two or four valves. The ovary is generally superior, with one locule and one ovule, and the fruit, a one-seeded berry, sits either free on a pedicel, is partially enclosed by persistent tepals or the receptacle, or is entirely enclosed by the receptacle.

Classification of Lauraceae

Strictly speaking, there is no lack of suprageneric classifications of Lauraceae. All have in common one characteristic: they are not widely accepted. We will present a brief review of these classifications and list the main characters used in making them. The position of *Cassytha* in the different classifications will not be discussed; it is always separated from the other Lauraceae because of its herbaceous, parasitic habit, and we place it in its own subfamily, the Cassythoideae.

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Characters Used in Nees (1836) Classification

1) Leaves deciduous vs. evergreen.
  2) Inflorescence umbellate or glomerate.
    a) Inflorescence umbellate, involucrate.
    b) Inflorescence glomerate or subracemose, arising from perulate buds.
  2) Inflorescence paniculate.
    3) Anthers opening apically.
    3) Anthers opening below tip, equal.
    3) Outer anthers petaloid.
    3) Anthers with distinct filaments.
      4) Fruits covered by perianth tube.
      4) Fruits not protected by perianth tube.
        5) Staminodia lacking or, if present, without capitate apex.
        5) Staminodia with triangular head.
          6) Tepals entirely persistent
            7) in a solid cup
            7) spreading, not thickened
          6) Tepals largely deciduous
            7) Truncate base,only, persistent.
            7) Entirely deciduous.

Figure 1. Main characters used in Nees's (1836) classification.

Meissner

1) Suborder Laurineae
2) Suborder Gyrocarpeae, excluded from Lauraceae
3) Suborder Cassytheae, *Cassytha*

Laurineae:

A. Inflorescence paniculate, racemose or spicate. No involucres.
Tribus Perseaceae:
Flowers hermaphrodite. Stamens 9. Cupule present or lacking. Staminodia well developed.
  1) 4-celled anthers; 6 genera
  2) 2-celled anthers; 6 genera
Tribus Oreodophneae:
Flowers unisexual, cupule present or lacking.
  a) Stamens free, 4-celled, inner 3 extrorse; 7 genera (*Ocotea* s.l., *Nectandra*, *Pleurothyrium*)
  b) Stamens free, 4-celled, all introrse; 2 genera (*Sassafras*, *Sassafridium*)
  c) Stamens free, 2-celled, inner 3 extrorse; 1 genus (*Goeppertia*)
  d) Stamens fused, flowers hermaphrodite; 2 genera (*Symphysodaphne*, *Synandrodaphne*)
Tribus Cryptocaryeae:
Flowers hermaphrodite, fruits enclosed in calyx.
  1) Flowers 4-merous. *Adenostemum*, excluded.
  2) Flowers 3-merous, 2-celled. 10 genera, including: *Cryptocarya*, *Aiouea*, *Ampelodaphne*
  3) Flowers 3-merous, capitate, 2-celled; stamina monadelphic. *Misantheca*.
  4) Flowers 3-merous, 4-celled, stamens free. 4 genera
B. Flowers umbellate or glomerulate. Involucrum present.
Tribus Litseaceae:
  Subtribus Tetranthereae. Anthers 4-celled; 5 genera
  Subtribus Daphnidieae. Anthers 2-celled; 5 genera

Figure 2. Main characters used in Meissner's (1864) classification.

It has been suggested that *Cassytha* is closely related to *Cryptocarya* (Rohwer, 1993b); however, the main characters discussed in this paper (inflorescence structure and wood and bark anatomy) will not elucidate the relationsips of *Cassytha*. The classifications by Nees (1836; Fig. 1), Meissner (1864; Fig. 2), Bentham and Hooker (1880; Fig. 3), Pax (1889; Fig. 4), Mez (1889; Fig. 5), and Hutchinson (1964; Fig. 6) are all based on the following characters: inflorescence paniculate versus umbellate; number of anther cells (2 vs. 4); number of stamens; fruit enclosed in perianth versus seated in a cup or free; and flowers unisexual or bisexual. These classifications are strongly influenced by the choice of the most important character, and differences between the classifications are a result of such choices and are not based on new or better data. For instance, Pax used 2- versus 4-celled anthers as the most important character, while Mez and Nees used inflorescence paniculate versus racemose. None of these authors defends or explains his determination of the importance of the characters, and all classifications are in some aspects confusing. Several of these classifications include genera no longer recognized or which were based on faulty diagnoses, but such details are of historical interest only.

Kostermans (1957) published a new classification, in which he recognized five tribes (Fig. 7). One tribe was recognized by its involucrate inflorescence, the other four non-involucrate tribes by the development or lack of cupules. One tribe was recognized by a complete absence of a cupule (for example, *Persea* and *Beilschmiedia*), the second by the presence of a more or less cup-shaped cupule (*Ocotea*, *Nectandra*), the third by having the fruit almost completely enclosed by the cupule (*Cryptocarya*, for example), and the fourth by having a truly inferior ovary and the fruit entirely enclosed by the hypanthium (only *Hypodaphnis*). Further division within the tribes is primarily based on number of anther cells. In comparison with the contemporary classification of Hutchinson (1964), Kostermans's classification is clearly superior, not because the characters used for the classification are sounder, but because he knew the Lauraceae well. Thus, he excluded a number of weak genera recognized by Hutchinson, and avoided errors that Hutchinson, less experienced with Lauraceae, made. Kostermans's classification has found general acceptance during the last 30 years, although sev-

Bentham and Hooker (1880)

3 TRIBES

1) Perseaceae. Stamens of whorl III opening extrorse, with 2 basal glands, inflorescences lax, pedunculate.
   a) Anthers 2-celled. Fruit included in perianth.
   b) Anthers 2-celled. Fruit with / without cupule. subdivided by number of stamens.
   c) Anthers 4-celled.Fruit with/without cupule subdivided by number of stamens.

2) Litseaceae. Trees or shrubs. All stamens opening introrse. Inflorescence dense, short, subsessile (except Sassafridium).
   a) Inflorescence lax or imbricate - bracteate.
   b) Inflorescence umbellate or capitate, included in an involucre. Subdivided by number of anther cells.

3) Cassytheceae. Leafless vines.

Figure 3. Main characters in Bentham & Hooker's (1880) classification.

PAX

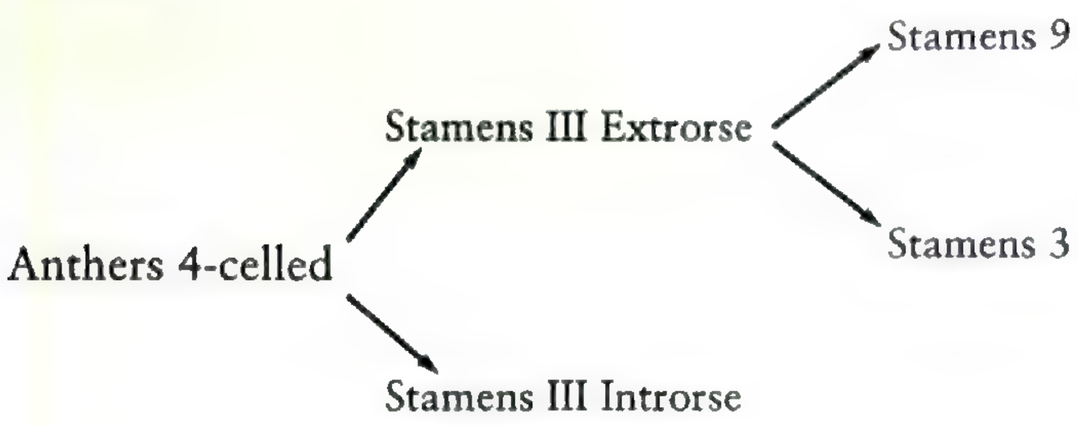

Figure 4. Main characters used in Pax's (1889) classification.

Mez

Herbaceous parasitic vine; inflorescence indeterminate ..... ***Cassytheae***
Shrubs or trees, inflorescence determinate ..... ***Laureae***
  Inflorescences paniculate, exinvolucrate ..... ***Perseeae***
    Anthers of outer two whorls 2-celled or sterile .....
    Anthers of outer two whorls 4-celled .....
  Inflorescences racemose, involucrate ..... ***Litseeae***
    Anthers 2-celled .....
    Anthers 4-celled .....

Figure 5. Main characters used in Mez's (1889) classification.

eral workers have pointed out difficulties with generic circumscription and classification (Hyland, 1989; Rohwer et al., 1991; van der Werff, 1991). Richter (1981) published the results of his study of wood and bark anatomy of Lauraceae, in which he found three large groupings of genera (Fig. 8). One of the groups corresponds with the tribe including genera with involucrate inflorescences, but the other two groups have no counterpart in the existing classifications. For instance, Richter placed *Cryptocarya* and *Beilschmiedia* in the same group, while in Kostermans's classification they occupy very different positions.

The most recent classification is by Rohwer (1993b). He recognized two main groups, based on inflorescence type, one involucrate and one exinvolucrate. Further divisions were based on fruit and floral characters, but because these characters were

Hutchinson

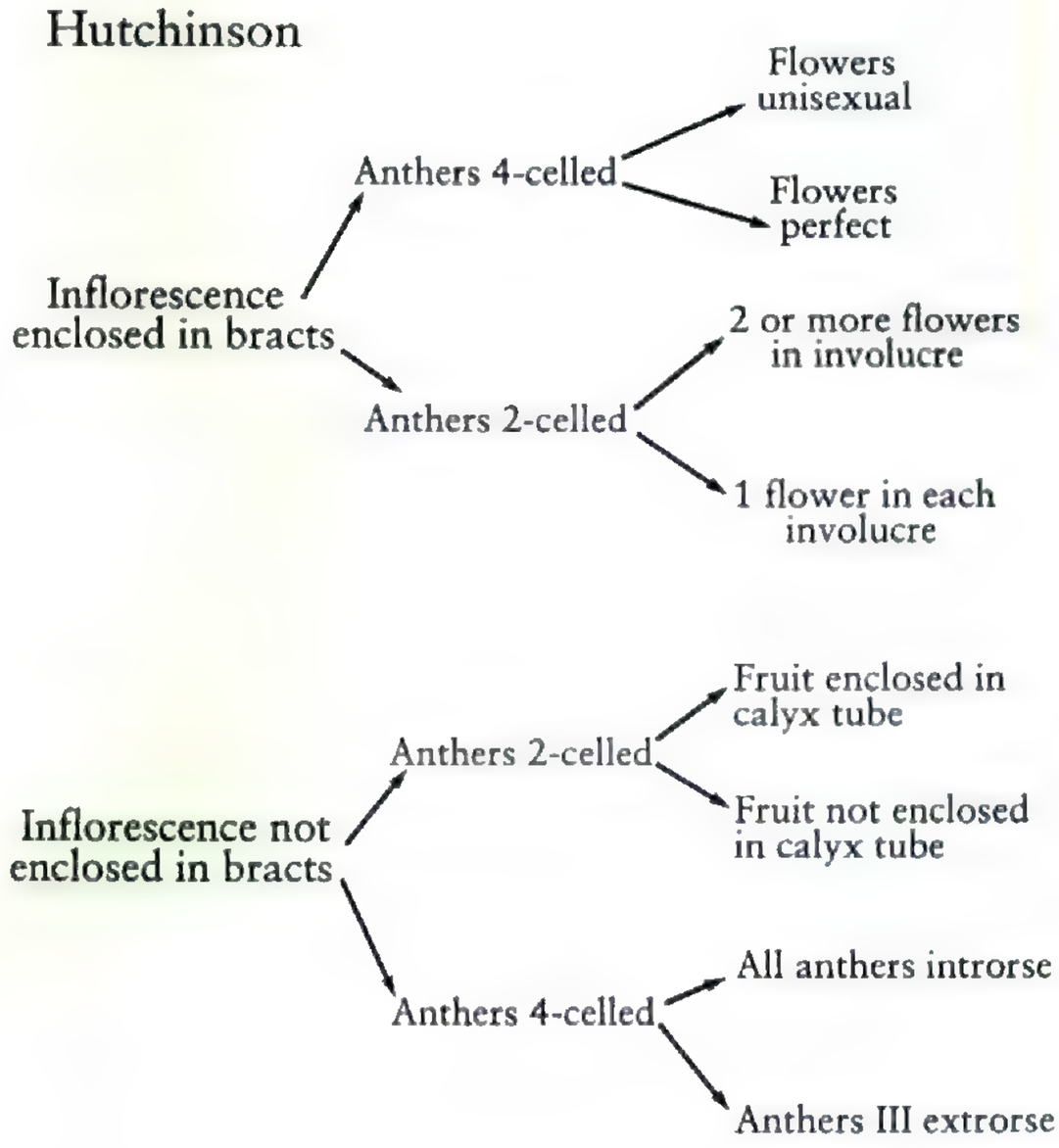

Figure 6. Main characters used in Hutchinson's (1964) classification.

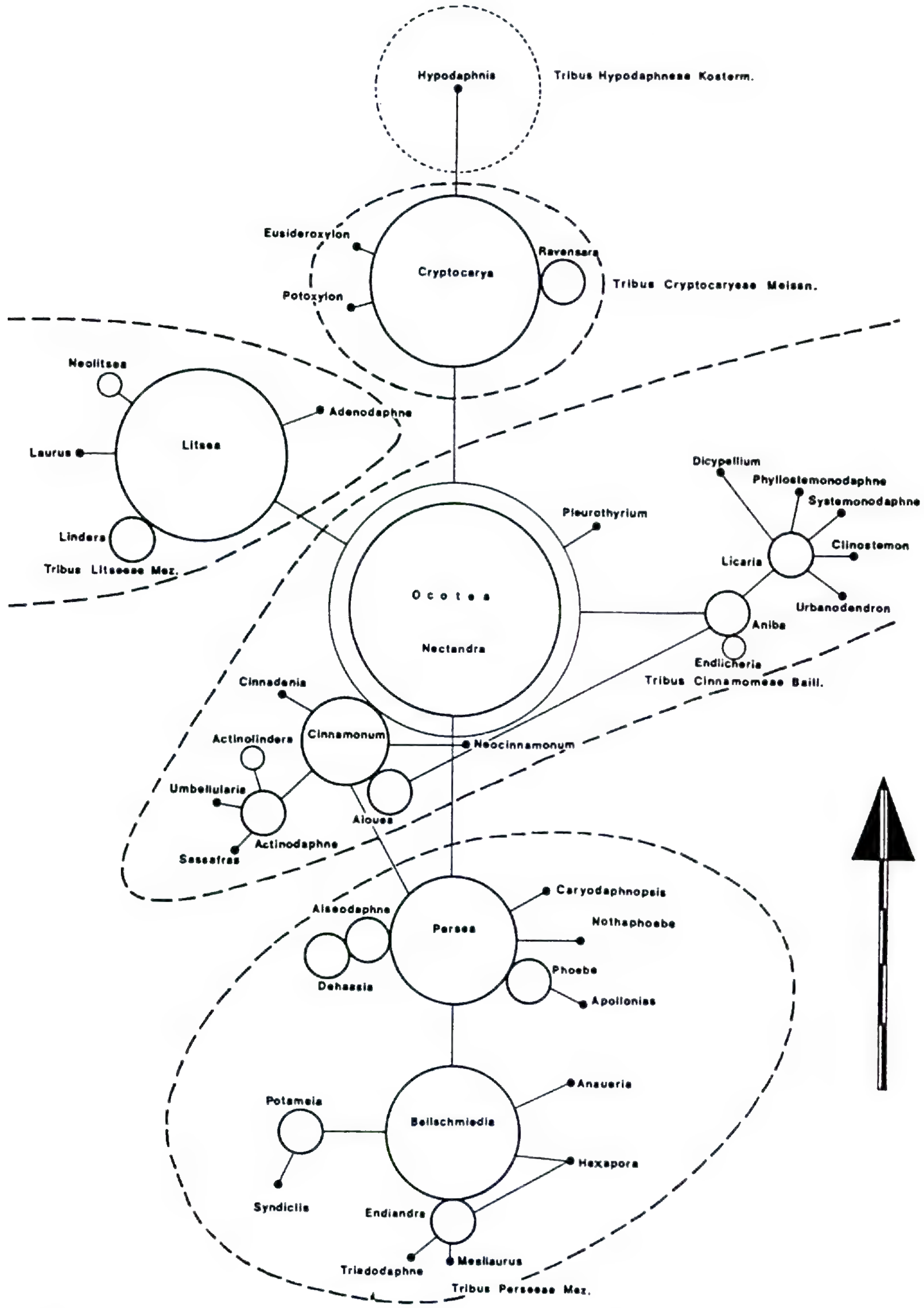

Figure 7. Classification of Kostermans (1957). Reprinted with permission.

used with some hesitation, no formal classification was proposed. Keys to genera were recently published by van der Werff (1991; for genera of the New World) and Rohwer (1993b; for genera worldwide).

Strength of Characters Used in Published Classifications

A robust classification demands that the characters used are reliable; that is, there are no or few

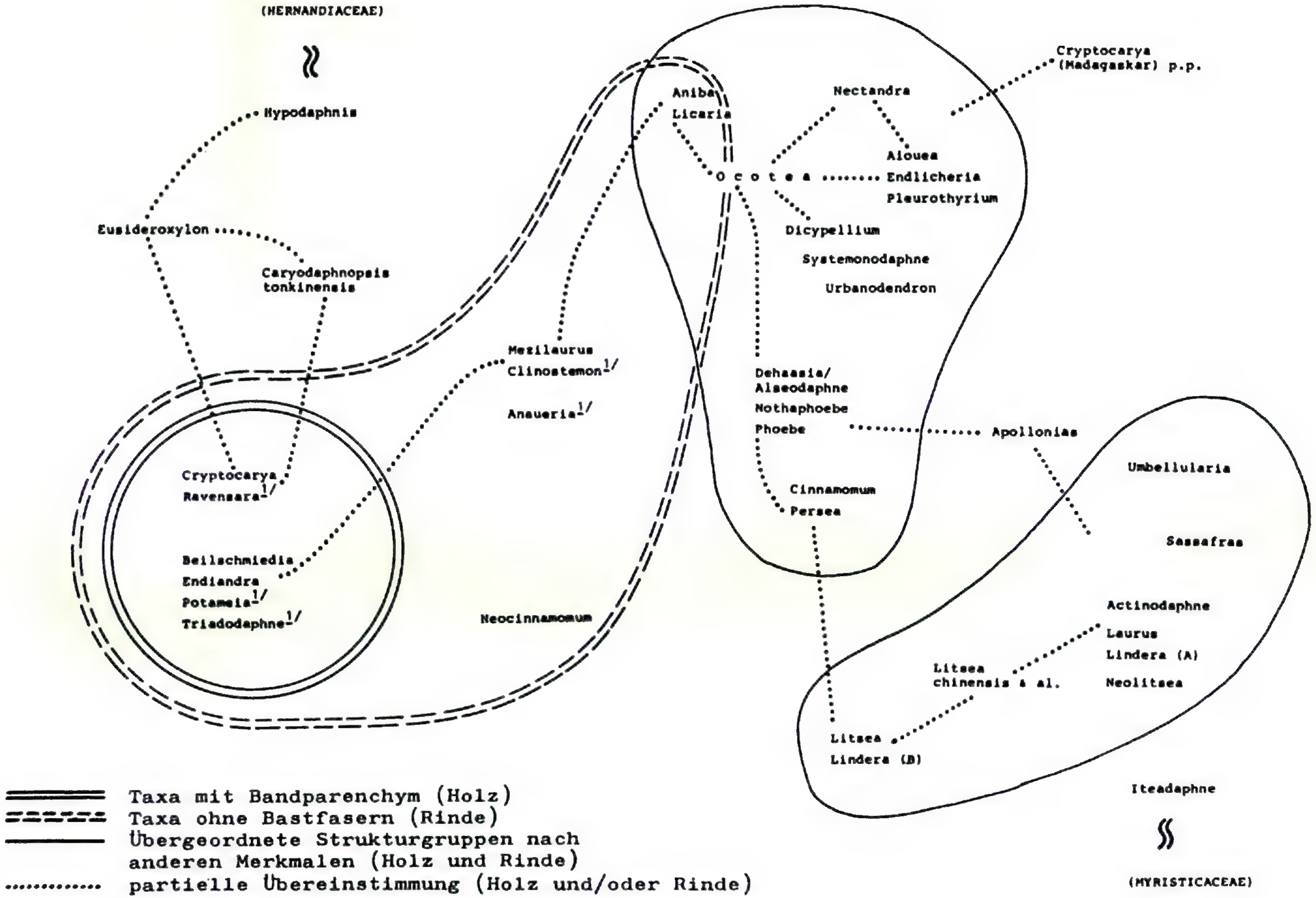

Abb. 52: Anatomische Gruppierungen in Lauraceen

Figure 8. Classification of Richter (1981).

Table 1. Genera with variation in number of anther cells.

Aiouea	normally nine 2-celled, rarely six or three 2-celled
Aniba	normally nine 2-celled, rarely six 2-celled
Aspidostemon	either six 2-celled or three 2-celled
Beilschmiedia	normally nine 2-celled, rarely six 2-celled or nine 1-celled
Caryodaphnopsis	normally nine 4-celled, rarely nine 2-celled or six 2-celled
Cassytha	normally nine 2-celled, rarely six 2-celled
Cinnamomum	normally nine 4-celled, rarely nine 2-celled
Endiandra	normally three 2-celled, rarely six 2-celled
Endlicheria	normally nine 2-celled, rarely six 2-celled + three 4-celled
Kubitzkia	nine 2-celled or six 4-celled + three 2-celled
Persea	normally nine 4-celled, rarely nine 2-celled or six 4-celled + three 2-celled
Potameia	normally four 2-celled, rarely four 1-celled or two 1-celled
Urbanodendron	normally nine 4-celled, rarely nine 2-celled

exceptions to the conditions characteristic for a given taxon. An analysis of the characters used most frequently in the generic and suprageneric classifications of Lauraceae will allow us to estimate how well these taxa are founded.

One frequently used character refers to the inflorescence. It is phrased in slightly different ways in the various classifications. Nees (1836) and Meissner (1864) contrasted umbellate versus paniculate inflorescence, with and without an involucrum; Hutchinson (1964) stressed the presence or absence of bracts; Kostermans (1957), decussate bracts; and Rohwer (1993b) mentioned "some kind of involucre." Based on the senior author's experience, the character states of involucrate, racemose versus exinvolucrate, paniculate inflorescence are reliable; we know of no genera in which both kinds of inflorescence are represented, and we accept the inflorescence differences as reliable generic characters. The importance of inflorescence types in the classification of Lauraceae will be discussed further in this article.

The next set of frequently used characters are those of the androecium, i.e., the number of fertile stamens and number of anther cells on each stamen. Possible variation of these characters can, of course, best be studied in genera defined by something other than these androecial characters. This variation is considerable (Table 1). For instance, among the neotropical species of *Caryodaphnopsis*, defined by having opposite leaves and unequal tepals, are species with nine 4-celled stamens, nine 2-celled stamens, and six 4-celled stamens plus three staminodia. Likewise, most species of *Potameia*, defined by having dimerous flowers, have four 2-celled stamens; a few have four 1-celled stamens and one species, as yet undescribed, has two 1-celled stamens. Neotropical species placed in *Persea* mostly have nine 4-celled stamens, but some have nine 2-celled stamens or six 4-celled and three 2-celled or six 4-celled and three staminodia. Looking at the genera defined by 2-celled stamens, the similarity between most *Aiouea* species (2-celled) and *Cinnamomum* (4-celled) is striking and seems more than convergence; however, *Aiouea vexatrix* van der Werff is very similar to some sympatric *Ocotea* species, as are *A. lundelliana* Allen and *A. costaricensis* (Mez) Kostermans (van der Werff, 1987a, 1988; Rohwer et al., 1991). A similar situation is found in *Endlicheria* (two-celled). Some of its species are strikingly similar to *Rhodostemonodaphne* or *Ocotea* species (Rohwer et al., 1991). A third generic pair is formed by *Mezilaurus* (2-celled) and *Williamodendron* (4-celled); species of *Williamodendron* were initially described as *Mezilaurus* (van der Werff, 1987), but were subsequently recognized as a distinct genus (Kubitzki & Richter, 1987). A few other examples are presented in Table 2. On the other hand, there are also 2-celled genera that do not have a 4-celled counterpart, such as *Cryptocarya*, *Beilschmiedia*, *Aniba*, and *Licaria*. These examples indicate that the androecial characters often vary within genera and are

Table 2. "Genus" pairs in which apparently closely related species or species groups are placed in different genera due to generic circumscription by anther cell number.

4-celled	2-celled
Cinnamomum	*Aiouea*
Cinnamomum	*Temmodaphne*
Ocotea	*Aiouea*
Ocotea	*Endlicheria*
Rhodostemonodaphne	*Endlicheria*
Williamodendron	*Mezilaurus*
Litsea	*Lindera*
Parasassafras	*Sinosassafras*

unreliable characters in classification at generic and higher levels.

The only character of the gynoecium frequently used is the degree to which the fruit is covered by the hypanthium—from no cover and fully exposed to a completely inferior ovary and the fruit fused with the hypanthium. In most genera this character is constant; exceptions occur in *Ocotea*, which includes species with pronounced cup-shaped cupules and species with very small, platelike cupules. In general though, the gynoecium character promises to be useful in generic and suprageneric classifications, because of its constancy at the generic level.

Earlier classifications were attempts to order the taxa being studied and were, in fact, frequently keys translated into a hierarchical system. A classification was a system enabling one to make identifications, and if that goal was met, the classification was acceptable.

More recently, the idea that classifications should reflect relationships and evolution of the taxon to be classified has found wide acceptance. Whether or not a phylogenetic classification is helpful in the identification process is less important. It is important to be aware of the dual purpose of a classification—on the one hand a path to identification, on the other a reflection of the phylogeny. For purposes of identification, the androecial characters are very useful because they are well defined and readily observed. On the other hand, characters such as number of stamens or number of anther cells are variable in several genera. This can only be observed in genera that can be defined by other characters. For instance, *Caryodaphnopsis* can be recognized by having opposite leaves and strongly unequal tepals; it also has very distinct wood anatomical characters. Within *Caryodaphnopsis* are species with nine 4-celled, nine 2-celled, and six 2-celled stamens. Other genera, for example, *Ocotea*, lack non-androecial characters (*Ocotea* is defined by having nine 4-celled stamens, with the cells in two horizontal rows), and species that resemble *Ocotea* very closely, but with 2-celled instead of 4-celled stamens, are placed in different genera (van der Werff, 1988; Rohwer et al., 1991). Genera such as *Caryodaphnopsis*, whose species share several non-androecial characters, can be expected to be monophyletic, but genera such as *Ocotea*, whose species only share androecial characters, are not likely to be monophyletic. Problems with classification of Lauraceae exist at two levels: there is a need for better defined, monophyletic genera, and a need for a phylogenetic classification at the suprageneric level. The focus of the rest of this paper is a more natural classification at the suprageneric level; it is acknowledged that this will not immediately lead to monophyletic genera, or to easier identifications.

Outlook for a Phylogenetic Classification

As has been discussed, the existing classifications are largely based on floral characters. The androecial characters vary frequently within genera and are therefore a poor choice as main characters for a generic and suprageneric classification. The gynoecial character emphasized by Kostermans does not vary within genera and holds more promise. However, the classification based on this character differs greatly from the generic groupings using wood and bark anatomy.

It seems unlikely that a thorough reexamination of floral and fruit characters will yield data with which a more robust classification can be constructed. Incorporating new data sets in building a classification looks like a more promising approach. Such an approach requires extensive collaboration between participating specialists. A few years ago, such a project was proposed and initiated by B. Hyland and the senior author, and will incorporate data from DNA studies, wood and bark anatomy, leaf oils, leaf venation and leaf cuticles, fruit anatomy, pollen, inflorescence types, and the traditional flower and fruit morphology into a new classification.

The published results of the study of wood and bark anatomy by the junior author (Richter, 1981), and the senior author's observations of inflorescence structures, both indicate that the Lauraceae are divided into three groups of genera. Wood and bark features employed are of an exclusively qualitative nature, quantitative characters being excluded as less reliable for their intrinsically high variation. They were selected and weighted in a function of their diagnostic value (identification) and discriminatory power (classification) within the specific context of Lauraceae. The set of secondary xylem characters includes primarily those relating to axial parenchyma distribution, fiber morphology, inorganic compounds, and vessel morphology. Secondary phloem characters considered as highly diagnostic and discriminating refer mainly to mechanical tissues, i.e., presence versus absence and morphology of phloem fibers and sclereids. These features were employed both in the positive (present) and negative affirmative (absent) sense. Group definitions are never based on any single feature, but on a combination of lead characters supported by secondary features of lesser diagnostic and/or discriminatory value.

Figure 9. Inflorescence types of group 1.

In the following, observations on inflorescence types are described and complemented by evidence derived from wood and bark structure:

1. Tribe Laureae. A number of genera have a racemose inflorescence; each flower has one bracteole at the base of the pedicel. Frequently, the inflorescence axis is shortened, with the inflorescence appearing umbellate. The inflorescences are

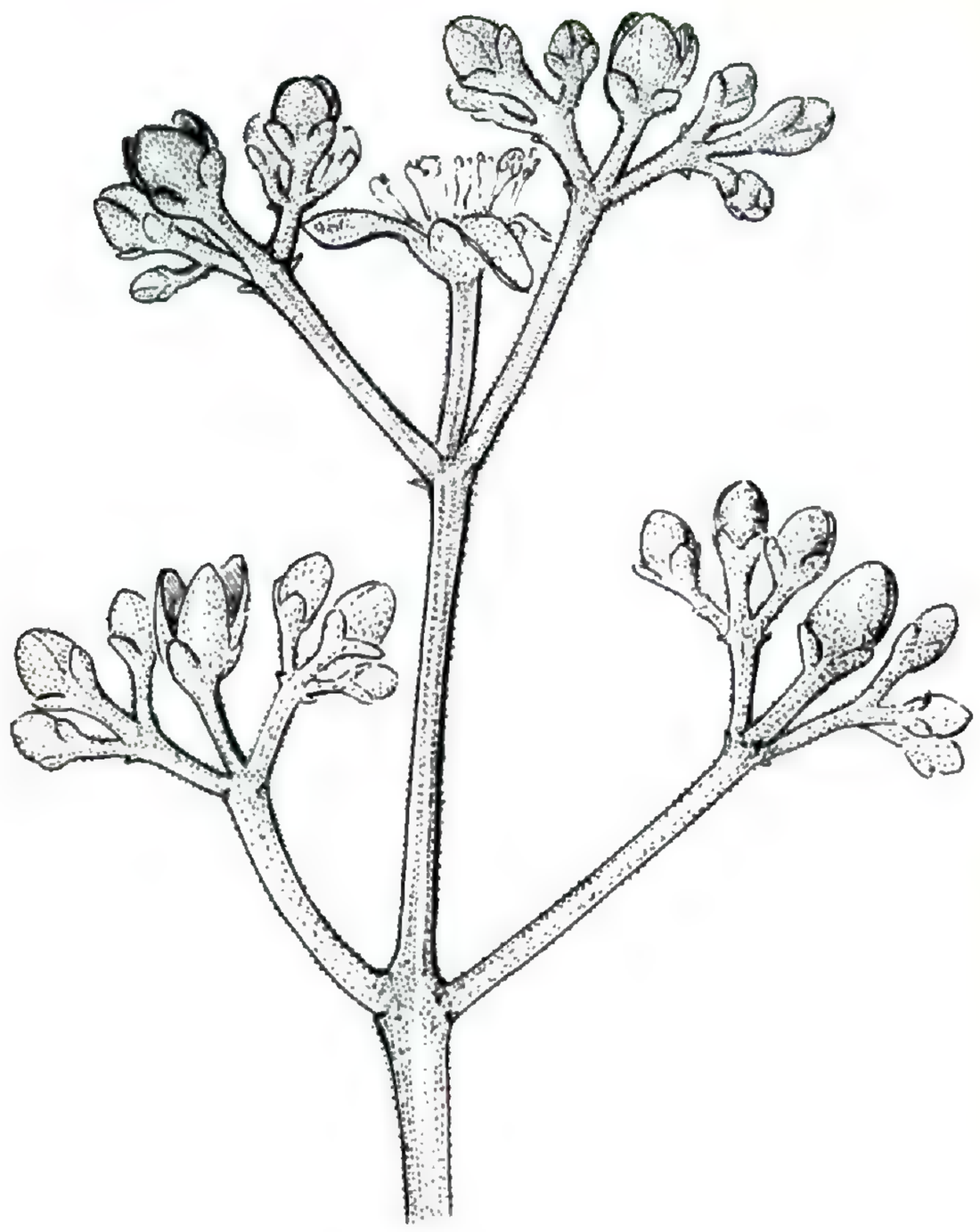

Figure 10. Inflorescence types of group 2.

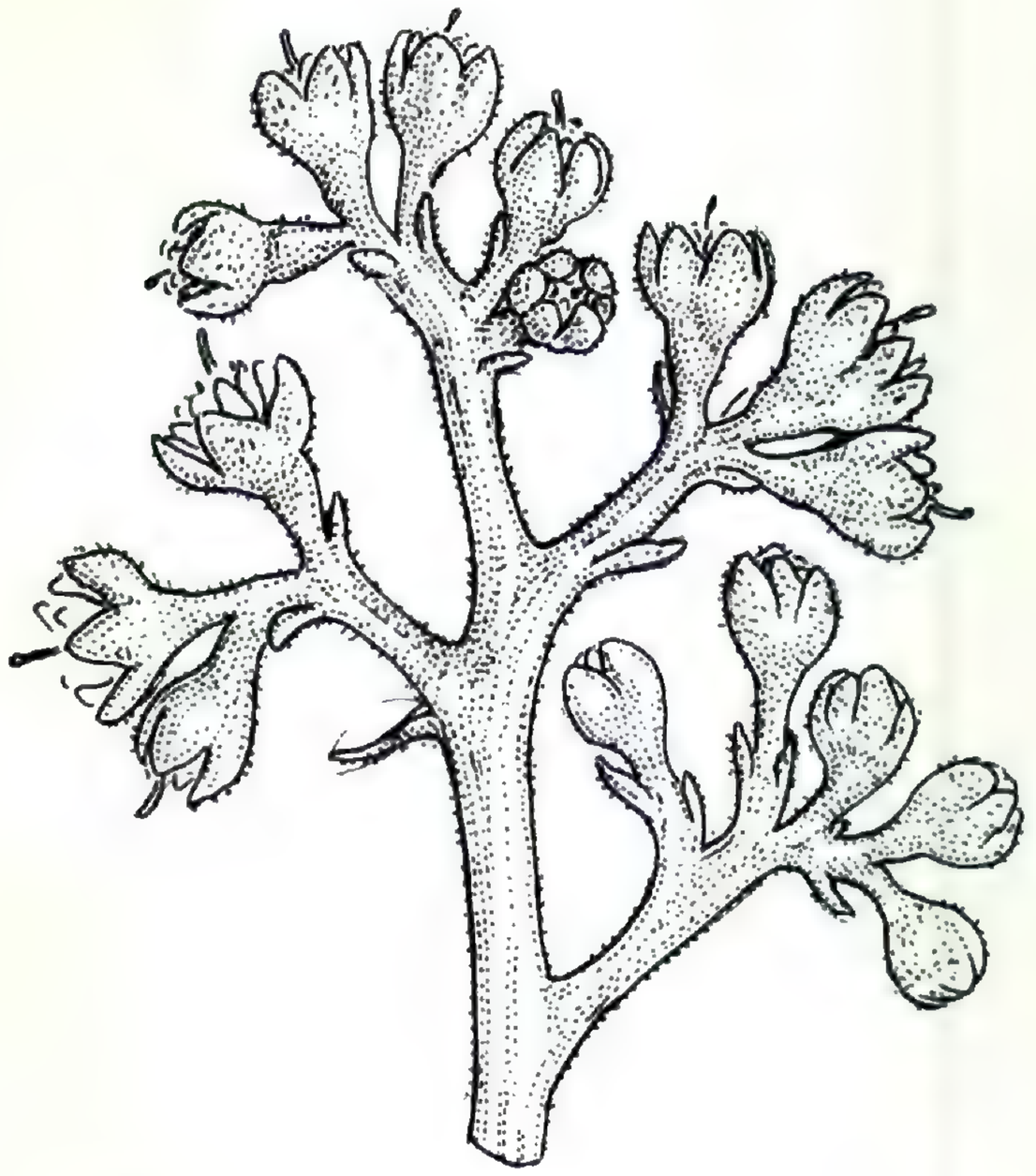

Figure 11. Inflorescence types of group 3.

often protected by a number of bracts (decussate or alternate). This group, with some modifications, has been recognized in nearly all classifications. It includes genera such as *Litsea, Lindera, Laurus,* and *Sassafras,* for instance (Fig. 9).

In terms of wood and bark structure, the group is characterized by the absence of marginal parenchyma and, in most instances, of septate fibers. Conversely, phloem fibers are always present. Further subunits can be recognized, for example the genus *Sassafras* on account of its accentuated growth ring structure, unique in Lauraceae and reflected in both secondary xylem ("ring porous") and phloem (distinct layering by early and late formed tissue strata).

2. Tribe Perseeae Nees. This group has a paniculate-cymose inflorescence. The initial branching of the inflorescence is paniculate, with alternate or opposite branches, while the flowers are arranged in cymes. The lateral flowers of a cyme are strictly opposite. At some point along the pedicel, two opposite bracts are present, frequently near the middle, but sometimes near the base. Included in this group are most neotropical genera (e.g., *Ocotea, Nectandra, Aniba, Licaria, Pleurothyrium*) and some neotropical/Asian genera (e.g., *Persea, Cinnamomum, Phoebe,* and *Dehaasia*) (Fig. 10).

Wood and bark structure depicts a group of genera characterized by the absence of marginal parenchyma and the ubiquitous presence of septate fibers (secondary xylem). Phloem fibers constitute part of the secondary phloem of nearly all taxa attributed to this group except some species of *Aniba, Licaria,* and *Ocotea* (Richter, 1981, 1985).

3. Tribe Cryptocaryeae Nees. The third group is formed by genera with a paniculate-± cymose inflorescence. At first glance these inflorescences look much like those of group 2, but the ultimate divisions are not strictly cymose. The lateral flowers of a "cyme" are not quite opposite, and flowers can appear individually placed along an inflorescence axis. The placement of bracts along the pedicels is variable in this group. Sometimes only one bract is present, sometimes two alternate or (sub)opposite ones; further observations are needed. This group includes such genera as *Beilschmiedia, Cryptocarya, Endiandra, Potameia,* and *Triadodaphne* (Fig. 11).

Wood and bark structure supports this circumscription of the *Beilschmiedia/Cryptocarya* assembly. All taxa share a number of distinctive features, such as the presence of marginal parenchyma, nonseptate fibers with conspicuously bordered pits, and exclusively simple vessel perforations in the secondary xylem. Conversely, in the secondary phloem the lack of fibers combines with characteristic sclereid formation.

As far as wood and bark structure is concerned, not all taxa can be satisfactorily accommodated in the three groups described above. *Cinnamomum* and *Persea,* for instance, appear to be transitional

between Group 1 and Group 2, with closer affinities to the latter. Similarly, *Mezilaurus* (including *Clinostemon*), an easily defined and recognized taxon, shares diagnostic bark characters with Group 3 and diagnostic wood characters with Group 2. Other, mostly small genera with a very distinctive wood and bark structure do not fit well with any of the three groups, though certain affinities can be recognized, for instance, in the case of *Caryodaphnopsis, Eusideroxylon/Potoxylon,* and *Hypodaphnis* with Group 3, of *Aspidostemon* and *Chlorocardium* with Group 2, and of *Iteadaphne* with Group 1.

Biogeographically, this division in three groups of genera is more logical than the generic alliances proposed in earlier classifications. The Laureae, with racemose inflorescences, are best represented, at the generic level, in the Northern Hemisphere (*Laurus, Sassafras, Umbellularia, Parasassafras, Litsea, Lindera, Neolitsea*), although several genera are well represented in the Asian tropics and a few extend into Australia. Most genera with unisexual flowers (about 10) belong to this group, and it includes genera with four and two anther cells. The Perseeae are mostly neotropical, with the genera in the *Persea–Cinnamomum–Phoebe* complex also present in tropical and subtropical (Northern Hemisphere) Asia; *Ocotea* is also present in Africa and Madagascar. Only three genera in this group have unisexual flowers; one of these, *Ocotea,* also includes many species with bisexual flowers. Both genera with 2-celled and 4-celled stamens are part of this group. The Cryptocaryeae are best represented in the Southern Hemisphere (*Cryptocarya, Beilschmiedia, Endiandra, Potameia*), but are also present in the Northern Hemisphere. All genera in this group have bisexual flowers. The core genera (*Cryptocarya, Beilschmiedia, Endiandra, Potameia, Triadodaphne*) have all 2-celled stamens; *Hypodaphnis, Eusideroxylon,* and *Potoxylon,* provisionally placed in this group, have 4-celled anthers.

Although not all genera can be satisfactorily placed in Richter's system, it avoids several anomalies present in Kostermans's classification, such as treating *Endiandra, Mezilaurus, Persea,* and *Beilschmiedia* as close relatives.

Thus, the two recent classifications of Lauraceae differ greatly from one another. Kostermans's (1957) classification is based mainly on one character only, the position of the gynoecium relative to the hypanthium, while Richter's (1981) classification is based on several characters from bark and wood and is supported by observations on inflorescence types. Although not all genera can be placed in our proposed tribal groupings (data are not yet available for some small genera and some genera have small, few-flowered inflorescences, making an interpretation of the inflorescences difficult), the fact that two greatly different sets of data support this classification makes this the best classification at hand, and the one to be tested when additional data become available.

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THE USE OF CUTICULAR FEATURES IN THE TAXONOMY OF THE LAURACEAE[1]

D. C. Christophel[2], *R. Kerrigan*[2], *and A. I. Rowett*[3]

ABSTRACT

The Lauraceae, with more than 2500 species in over 50 genera, and with the general lack of agreement in their recent classification, make an ideal candidate for a global study based on leaf cuticles. A technique for preparing cuticles is presented, and three types of characters of use in such studies (cell form, stomatal complex, and special cell types) are discussed. Preliminary results demonstrate the utility of these cuticular characters in defining genera such as *Endiandra* and *Beilschmiedia* and in sorting out biogeographical anomalies, such as found in *Caryodaphnopsis*, where the cuticles confirm placement of disjunct species within one genus. Potential challenges/problems posed by larger genera such as *Litsea*, *Cryptocarya*, *Cinnamomum*, *Ocotea*, and *Nectandra* are discussed.

Two of the most recent classifications of the Lauraceae are those of Kostermans (1957) and Rohwer (Kubitzki et al., 1993). The former is based on his own life-long studies, and the latter relies heavily on Kostermans and on the wood anatomical studies of Richter (1981), as well as including studies (primarily South American) by the author himself. The problems associated with these and other classifications of the Lauraceae are discussed by van der Werff and Richter (1996, this issue). From that review it is clear that further work is required to arrive at a satisfactory, or at least widely acceptable, classification of the family. Cuticular, and to a smaller degree, leaf architectural studies form one module in a multifaceted study of the generic delimitations of this family currently in progress.

The aim of this study is to analyze cuticular features for selected Lauraceae species whose generic positions have been predetermined by others, and in some cases questioned. At this time, no attempt has been made to use these features to confirm or disprove the evolutionary position, or indeed the "monophyly" (sensu cladistics), of these groups of Lauraceae. Consistent with that, individual features are not weighted or equalized, but are simply examined in light of the hypotheses generated by the placement of the species in genera by earlier workers. Characters that have shown consistency in this study are being included by the first author in the global generic revision of the Lauraceae, which follows on from this project. Even in that study, the primary aim will be to place groups of species in consistently recognizable genera, and not necessarily to propose phylogenetic relationships (cladistic or otherwise).

Cuticular studies of the Lauraceae are not novel. As early as 1926, Bandulska presented a study of fossil and extant Lauraceae and described some species of the former based on cuticular similarities to certain extant species. More recently, Hill (1986) discussed those features of the cuticle that allowed identification of Lauraceae, and placed the 12 species of fossil Lauraceae found in the Eocene Nerriga deposit within the form genus *Laurophyllum* based on these cuticular features. He made no attempt to place them relative to extant genera. Christophel and Rowett (in press) present descriptions of leaf architecture and cuticles of all species of leafy Lauraceae found in Australia. They also present a dichotomous key to cuticular features that allows identification to the generic (or to a species group within genus) level.

While most of the genera occurring in Australia can be clearly defined (extant leafy genera found there include *Beilschmiedia*, *Cinnamomum*, *Cryptocarya*, *Endiandra*, *Lindera*, *Litsea*, and *Neolitsea*), a notable exception is *Cryptocarya*. Although its species do not intermingle with those of any other

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genus, no set of characters has been found that holds all species together and yet separates the genus from others (Christophel & Rowett, in press). The result is that five groups of species key out to *Cryptocarya* in different parts of the key. Unfortunately, these five groupings do not correspond to those of Hyland (1989). This discrepancy indicates that further study of *Cryptocarya* is warranted, with the possibility existing that the genus as now defined is not natural and perhaps even polyphyletic. The heterogeneity, and perhaps artificiality of this large genus, has been previously suggested based on other features (e.g., Rohwer in Kubitzki, 1993).

In both the systems of Kostermans (1957) and of Rohwer (1993), the genera occurring in Australia are well spread across the major subfamilial groupings, and hence the mainly successful generic separations of Christophel and Rowett (in press) suggest that their character set represents a good starting place for the global generic revision. Dichotomous keys in general (e.g., Christophel & Rowett, in press) suffer from the requirement that certain features must be used before other (perhaps more obvious) ones can be applied. Therefore, the results of the global revision will be presented as a computerized, multi-entry key. If genera such as *Cryptocarya* do not fall out more reasonably when a better sample of their species is included, then the polyphyletic nature of the genus will be supported.

Methods

The majority of the leaf samples used in this and the ensuing complete study have been provided, or at least have had their identifications confirmed, by either H. van der Werff, Missouri Botanical Garden (MO) or B. P. M. Hyland, Herbarium Australiense–Atherton (QRS), who are both participating in the global revision of the Lauraceae. Hence the consistency of identification is maximized. Samples were only taken from mature leaves, and 1-cm^2 pieces were taken from the near basal margin on the lefthand side of the leaf with the adaxial surface upward, to eliminate variation that might have been caused by sampling from different areas. At least three samples from two different collections were used whenever possible, although for some species only one collection could be obtained, in which case several leaves from it were used. A list of specimens studied is presented in Table 1.

While the technique for cuticle preparation is similar to that used by Christophel and Rowett (in press), it is described here for completeness. The pieces of leaf are placed in small test tubes and soaked in 70–95% ethanol for approximately 18 hours. Experiments have shown that no observable difference in either quality of preparation or speed can be detected in samples by varying the ethanol strength within the above range. The ethanol is then decanted off and 10 drops of 40% w/vol H_2O_2 and five drops of 90% ethanol are added to the test tube, which is then heated to gentle boiling in a water bath for 2–48 hours. The cooking can be judged complete when the sample has turned light yellow to white and when the cut edges of the cuticle can be observed to be peeling back from the leaf surface like the two covers of a book. At that point the sample can be removed from the test tube and placed in a watch glass or petri dish of water, where the "book covers" are pried open and the "pages" of the book, or the actual cellular material, can be brushed away with fine artists' brushes. If removal of cellular contents specimens at this stage proves difficult, the specimens can be returned to 70–90% ethanol for a further 12 hours, which usually renders them much easier to clean.

While no chemical reaction involving the ethanol and H_2O_2 is apparent, leaf pieces pre-soaked in this manner clear between three and four times faster than those not pretreated. It may be that the ethanol acts to break surface tension on the cells, thus facilitating entrance of the hydrogen peroxide into the tissue. This is supported by the fact that preparation of fresh leaf material, which is naturally hydrated, is not enhanced to the same degree by the pretreatment in ethanol as are dried specimens.

Cleaned cuticles can be quickly rinsed in 2% ammonia to adjust pH, and then stained in 0.1% Crystal Violet for 20–120 seconds, or until the cuticle appears uniformly light purple to the naked eye. Under the compound microscope, anticlinal cell walls should appear bright to dark purple, as should thickened cuticular ledges, but the lumens of the cells should not appear stained, or with only a slight tinge of purple. Overstained samples can be destained by rinsing in 90–100% ethanol. In general, understained slides are preferable to overstained ones, as various techniques, including interference contrast, can be used to compensate for lack of stain, but little can be done to observe obscured detail in overstained cuticles.

Stained cuticles can be mounted in phenol glycerin jelly. When the slides have set and excess jelly is cleaned from the coverslip with warm water and a razor blade, the coverslip can be ringed with nail varnish (polish) to retard dehydration. If more permanent mounting is desired, the stained cuticles can be dehydrated and mounted in a resin-based medium. However, the first author has had slides

Table 1. Specimens examined.

Species	Country	Collector & number
Aiouea guianensis Aublet	Brazil	G. T. Prance 4401
Aiouea guianensis Aublet	Guiana	Jansen Jacobs 1986
Beilschmiedia bancroftii (Bailey) C. White	Australia	B. Gray 3787
Beilschmiedia bancroftii (Bailey) C. White	Australia	B. Gray 3977
B. brunnea B. Hyland	Australia	B. Gray 3900
B. brunnea B. Hyland	Australia	B. Gray 1837
B. castrisinensis B. Hyland	Australia	B. Gray 1092
B. castrisinensis B. Hyland	Australia	B. Gray 3210
B. castrisinensis B. Hyland	Australia	B. Gray 4158
B. collina B. Hyland	Australia	B. Hyland 10104
B. collina B. Hyland	Australia	B. Gray 1605
B. elliptica C. White & Francis	Australia	B. Hyland 4128
B. obtusifolia (F. Muell. ex Meissner) F. Muell.	Australia	B. Gray 1279
B. obtusifolia (F. Muell. ex Meissner) F. Muell.	Australia	B. Gray 3978
B. oligandra L. S. Smith	Australia	B. Gray 595
B. oligandra L. S. Smith	Australia	B. Gray 1726
B. oligandra L. S. Smith	Australia	B. Gray 2786
B. peninsularis B. Hyland	Australia	B. Hyland 11572
B. peninsularis B. Hyland	Australia	B. Gray 3623
B. recurva B. Hyland	Australia	B. Gray 276
B. recurva B. Hyland	Australia	B. Gray 4201
B. tooram (Bailey) B. Hyland	Australia	B. Gray 2826
B. tooram (Bailey) B. Hyland	Australia	B. Gray 3700
B. volckii B. Hyland	Australia	B. Gray 3823
B. volckii B. Hyland	Australia	B. Gray 2923
Caryodaphnopsis henrii A. Shaw	China	Kunming Herb. 645874
C. tonkinensis (Lec.) A. Shaw	China	Kunming Herb. 0125
C. tonkinensis (Lec.) A. Shaw	Philippines	Ramos 1667
C. sp. nov.	Peru	Jaramillo 11930
Chlorocardium venenosum Rohwer et al.	Colombia	Cogollo 5153
Chlorocardium venenosum Rohwer et al.	Ecuador	Zak 3913
Cinnamomum baileyanum (F. Muell. ex Bailey) Francis	Australia	B. Hyland 2648
C. laubatii F. Muell.	Australia	B. Gray 315
C. laubatii F. Muell.	Australia	B. Gray 3923
C. laubatii F. Muell.	Australia	B. Gray 3925
C. oliveri Bailey	Australia	B. Hyland 3303
C. oliveri Bailey	Australia	B. Hyland 12456
C. propinquum Bailey	Australia	B. Gray 686
C. propinquum Bailey	Australia	B. Gray 921
C. sellovianum (Nees & Mart.) Kosterm.	Brazil	Harley 25261
C. sellovianum (Nees & Mart.) Kosterm.	Brazil	Duarte 9295
C. virens R. Baker	Australia	B. Hyland 12340
Cryptocarya sp.	Madagascar	Miller 3725
Cryptocarya sp.	Madagascar	Miller 3955
Cryptocarya sp.	Madagascar	Armbruster 3145
Endiandra acuminata C. White & Francis	Australia	B. Gray 1368
Endiandra acuminata C. White & Francis	Australia	B. Gray 1583
Endiandra acuminata C. White & Francis	Australia	B. Gray 2332
E. anthropophagoram Domin.	Australia	B. Hyland 11712
E. anthropophagoram Domin.	Australia	B. Gray 2951
E. bellendenkerana B. Hyland	Australia	B. Gray 2953
E. bellendenkerana B. Hyland	Australia	B. Gray 2072
E. bessaphila B. Hyland	Australia	B. Gray 1644
E. bessaphila B. Hyland	Australia	B. Hyland 10650
E. collinsii B. Hyland	Australia	B. Hyland 3570
E. collinsii B. Hyland	Australia	B. Hyland 11134

Table 1. Continued.

Species	Country	Collector & number
E. compressa C. White	Australia	B. Gray 1753
E. compressa C. White	Australia	B. Gray 3723
E. cooperana	Australia	B. Gray 3209
E. cooperana	Australia	B. Gray 3565
E. cowleyana	Australia	B. Gray 1818
E. cowleyana	Australia	B. Gray 4123
E. crassiflora C. White & Francis	Australia	B. L. Jones 1283
E. dichrophylla F. Muell.	Australia	B. Gray 2915
E. dichrophylla F. Muell.	Australia	B. Gray 3713
E. dielsiana Teschner	Australia	B. Hyland 13176
E. dielsiana Teschner	Australia	B. Gray 3890
E. discolor Benth.	Australia	B. Hyland 2996
E. discolor Benth.	Australia	B. Gray 3012
E. floydii B. Hyland	Australia	B. Hyland 4619
E. glauca R. Br.	Australia	B. Gray 3211
E. glauca R. Br.	Australia	B. Hyland 14039
E. globosa Maiden & E. Betche	Australia	B. Gray 3173
E. globosa Maiden & E. Betche	Australia	B. Gray 4152
E. grayi B. Hyland	Australia	B. Gray 3157
E. grayi B. Hyland	Australia	B. Gray 3726
E. grayi B. Hyland	Australia	B. Gray 4084
E. grayi B. Hyland	Australia	B. Gray 4162
E. hayesii Kosterm.	Australia	B. Hyland 4553
E. hypotephra F. Muell.	Australia	B. Gray 456
E. hypotephra F. Muell.	Australia	B. Gray 3969
E. hypotephra F. Muell.	Australia	B. Gray 4001
E. impressicosta Alenn	Australia	B. Gray 2454
E. impressicosta Alenn	Australia	B. Gray 3101
E. insignis (Bailey) Bailey	Australia	B. Gray 1641
E. insignis (Bailey) Bailey	Australia	B. Gray 3714
E. introrsa C. White	Australia	B. Hyland 12338
E. jonesii	Australia	B. Gray 2255
E. jonesii	Australia	B. Gray 2869
E. kingiana Gamble	Sarawak	B. Hyland 14146
E. leptodendron B. Hyland	Australia	B. Gray 3924
E. leptodendron B. Hyland	Australia	B. Gray 3953
E. limnophila B. Hyland	Australia	B. Hyland 12375
E. limnophila B. Hyland	Australia	B. Hyland 12377
E. longipedicellata C. White & Francis	Australia	B. Hyland 6256
E. longipedicellata C. White & Francis	Australia	B. Gray 3243
E. microneura C. White	Australia	B. Gray 3822
E. monothyra B. Hyland	Australia	B. Hyland 12584
E. monothyra B. Hyland	Australia	B. Gray 1647
E. monothyra B. Hyland	Australia	B. Gray 1652
E. monothyra B. Hyland	Australia	B. Gray 3284
E. monothyra B. Hyland	Australia	B. Gray 3673
E. montana C. White	Australia	B. Gray 2825
E. montana C. White	Australia	B. Gray 3127
E. muelleri Meissner in DC	Australia	B. Hyland 12330
E. muelleri Meissner in DC	Australia	B. Hyland 12957
E. muelleri Meissner in DC	Australia	B. Hyland 12972
E. palmerstonii (Bailey) C. White	Australia	B. Hyland 11721
E. phaeocarpa B. Hyland	Australia	B. Gray 3297
E. phaeocarpa B. Hyland	Australia	B. Gray 3873
E. pubens Meissner in DC	Australia	B. Gray 2971
E. sankeyana Bailey	Australia	B. Gray 3579
E. sankeyana Bailey	Australia	B. Gray 4103

Table 1. Continued.

Species	Country	Collector & number
E. sideroxylon B. Hyland	Australia	B. Gray 3904
E. sideroxylon B. Hyland	Australia	B. Gray 4148
E. sieberi Nees	Australia	B. Gray 1504
E. virens F. Muell.	Australia	B. Hyland 4602
E. wolfii B. Hyland	Australia	B. Gray 1328
E. wolfii B. Hyland	Australia	B. Gray 3962
E. xanthocarpa B. Hyland	Australia	B. Gray 1614
E. xanthocarpa B. Hyland	Australia	B. Gray 5155
E. sp.	Java	B. Hyland 14217
Litsea costalis (Nees) Kosterm.	Sembilon	B. Hyland 14130
Ocotea lentii Burger	Costa Rica	Moraga 171
Ravensara sp.	Madagascar	Miller 3835
Ravensara sp.	Madagascar	G. McPherson 14428
Rhodostemonodaphne grandis (Mez) Rohwer	French Guiana	Mori 20904
Rhodostemonodaphne grandis (Mez) Rohwer	Peru	Kroll 134
Rhodostemonodaphne grandis (Mez) Rohwer	Peru	Kayap 3541
R. kunthiana (Nees) Rohwer	Ecuador	Zak 4452
R. kunthiana (Nees) Rohwer	Costa Rica	Herrera 2397

mounted in glycerin jelly for 20 years without harm befalling them, and the advantages of that medium are that it is inexpensive, quick to use, and the cuticles can be retrieved by soaking the slide in hot water if other preparations or stain adjustments are to be made later. For long-term storage in a dry environment, dehydration will be better retarded by ringing slides in a wax. Safranin staining also provides good visual detail of the cuticles, but the red color necessitates the use of a green filter for maximum contrast with black-and-white photography, while the purple staining of Crystal Violet does not require this.

All cuticular photographs (Figs. 1–18, 20–25) were taken using a Zeiss automatic 35mm camera on a Zeiss Axioplan microscope with a 40× objective and 10× eyepiece.

Cuticular Characters

Leaf cuticular characters used to delimit genera in the Australian Lauraceae (Christophel & Rowett, in press) fall into three broad categories: (1) those of the walls of normal, non-stomatal cells, (2) those of the stomatal complex (including subsidiary cells), and (3) those of specialized cells such as trichomes, trichome bases, and hydathodes. The Lauraceae appear to be uniformly hypostomatic, and hence separate character sets can be used for the adaxial (upper) and abaxial (lower) cuticles. In practice, leaves of many species of Lauraceae appear to differ in their two cuticular surfaces, not only in presence/absence of stomata, but also in features of the indument and of general epidermal cell size and shape (e.g., Figs. 1, 2).

Considering first the features of non-stomatal cells, the periclinal walls can be seen to vary from densely papillose (Fig. 1) to lightly papillose (Fig. 3), granular (Fig. 2), punctate (Fig. 10), slightly striate (Fig. 6), or smooth (Figs. 14, 18). To be considered granular, the periclinal walls must be regularly and coarsely so. There are probably several subtly different states between coarsely granular

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Figures 1–6. —1. Abaxial cuticle of *Caryodaphnopsis henrii* A. Shaw, from L509, Botany Department Herbarium, Adelaide University; collected from the Kunming Botanical Institute Herbarium (#645874), Kunming, China. Collector and number in Chinese and not readable. Collection from Southern China. Magnification as per Figure 24.—2. Adaxial cuticle of *Caryodaphnopsis henrii* A. Shaw. All information and magnification as per Figure 24.—3. Abaxial cuticle of *Caryodaphnopsis* sp. nov. taken from L317, Botany Department Herbarium, Adelaide University, from *Jaramillo 11930* at MO, from Peru; magnification as per Figure 24.—4. Abaxial cuticle of *Caryodaphnopsis tonkinensis* (Lec.) A. Shaw from L508, Botany Department Herbarium, Adelaide University, from the Botanical Institute of Kunming, China, (sheet #0125); collected in southern China; magnification as per Figure 24.—5. Abaxial cuticle of *Chlorocardium venenosum* Rohwer, Richter & van der Werff taken from L398, Botany Department Herbarium, Adelaide University; originally from *Cogollo 5153* at MO; collected in Colombia. Scale bar as per Figure 20.—6. Adaxial cuticle of *Chlorocardium venenosum*. All details and magnification as per Figure 5.

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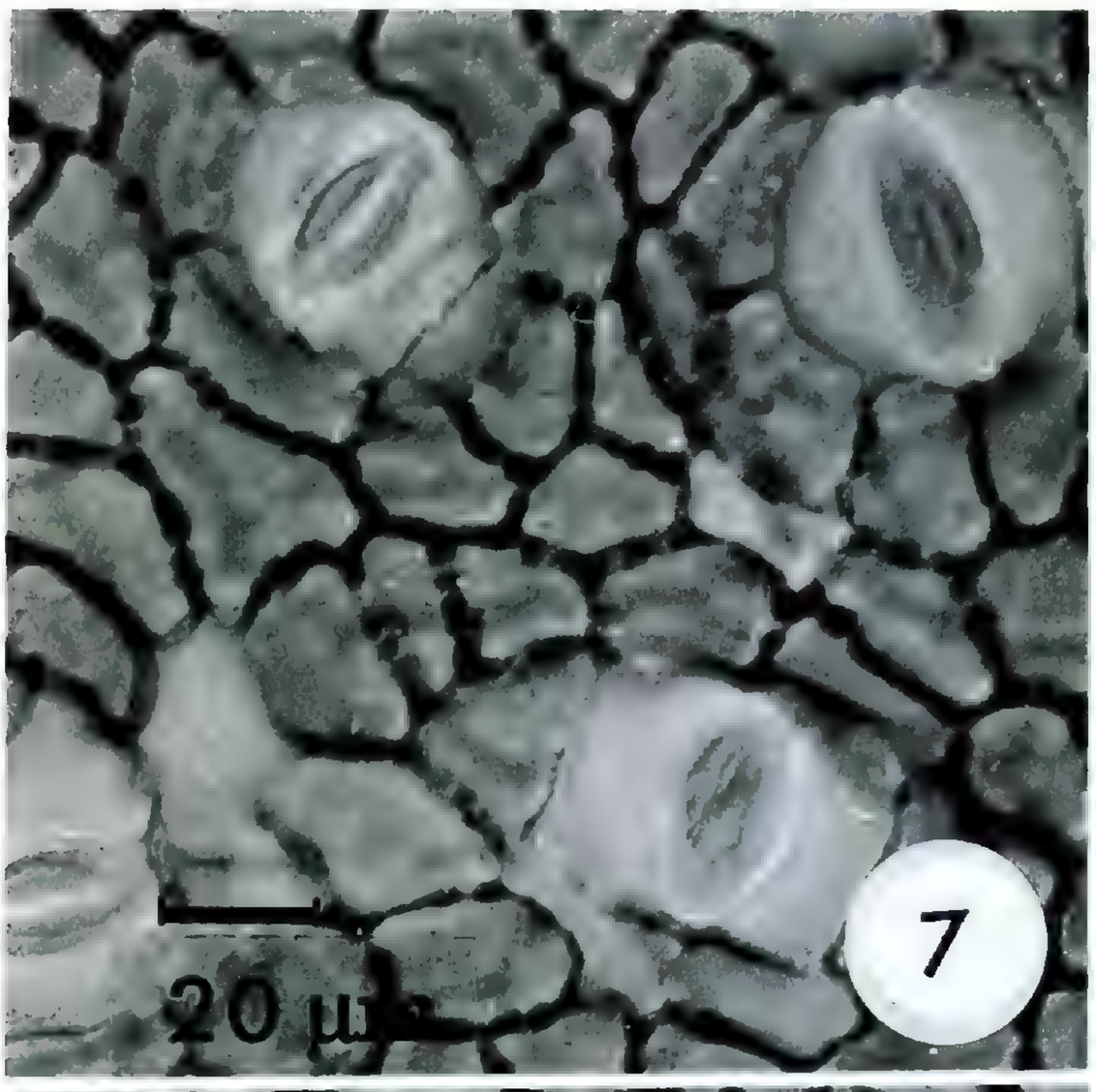
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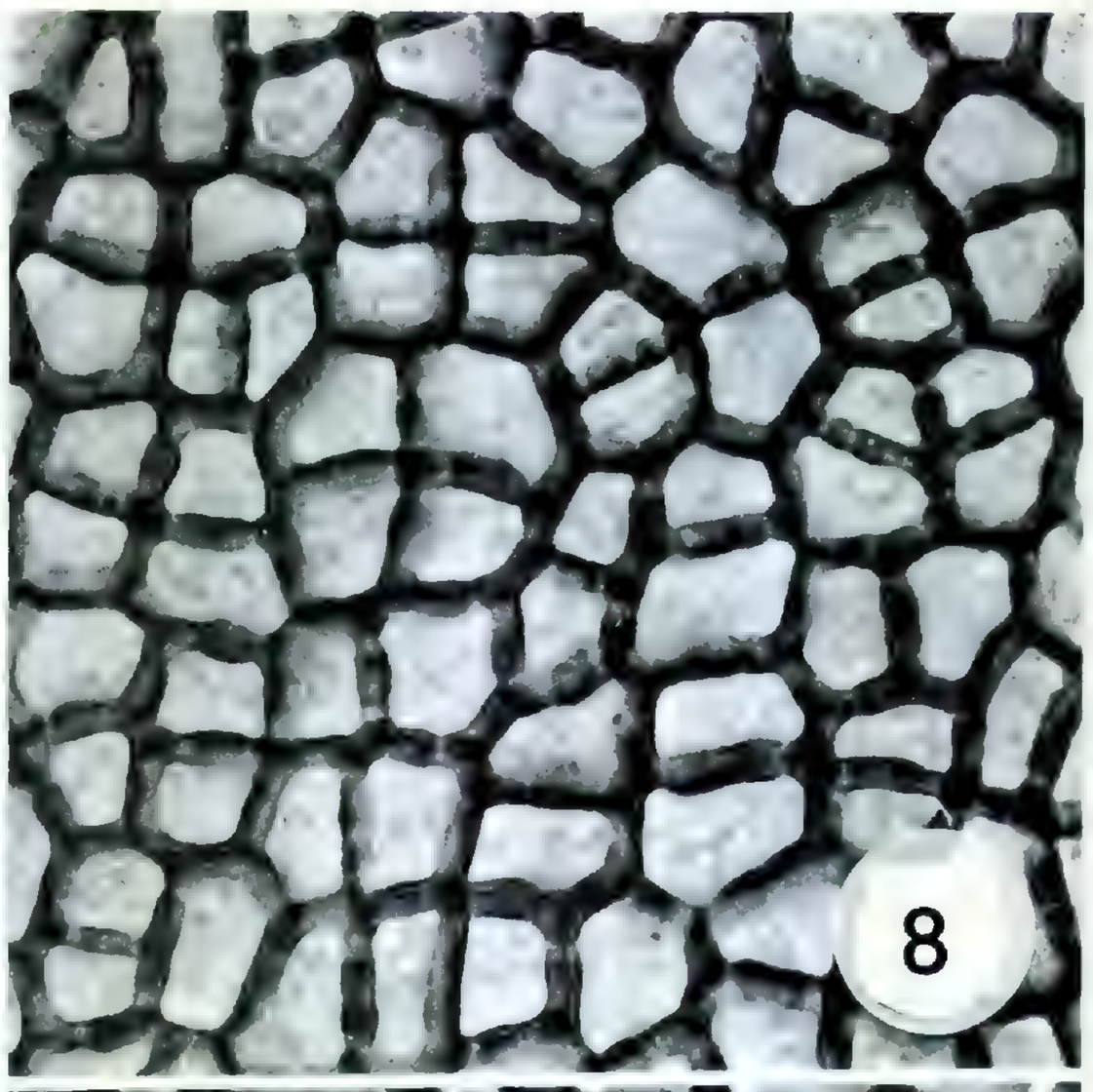
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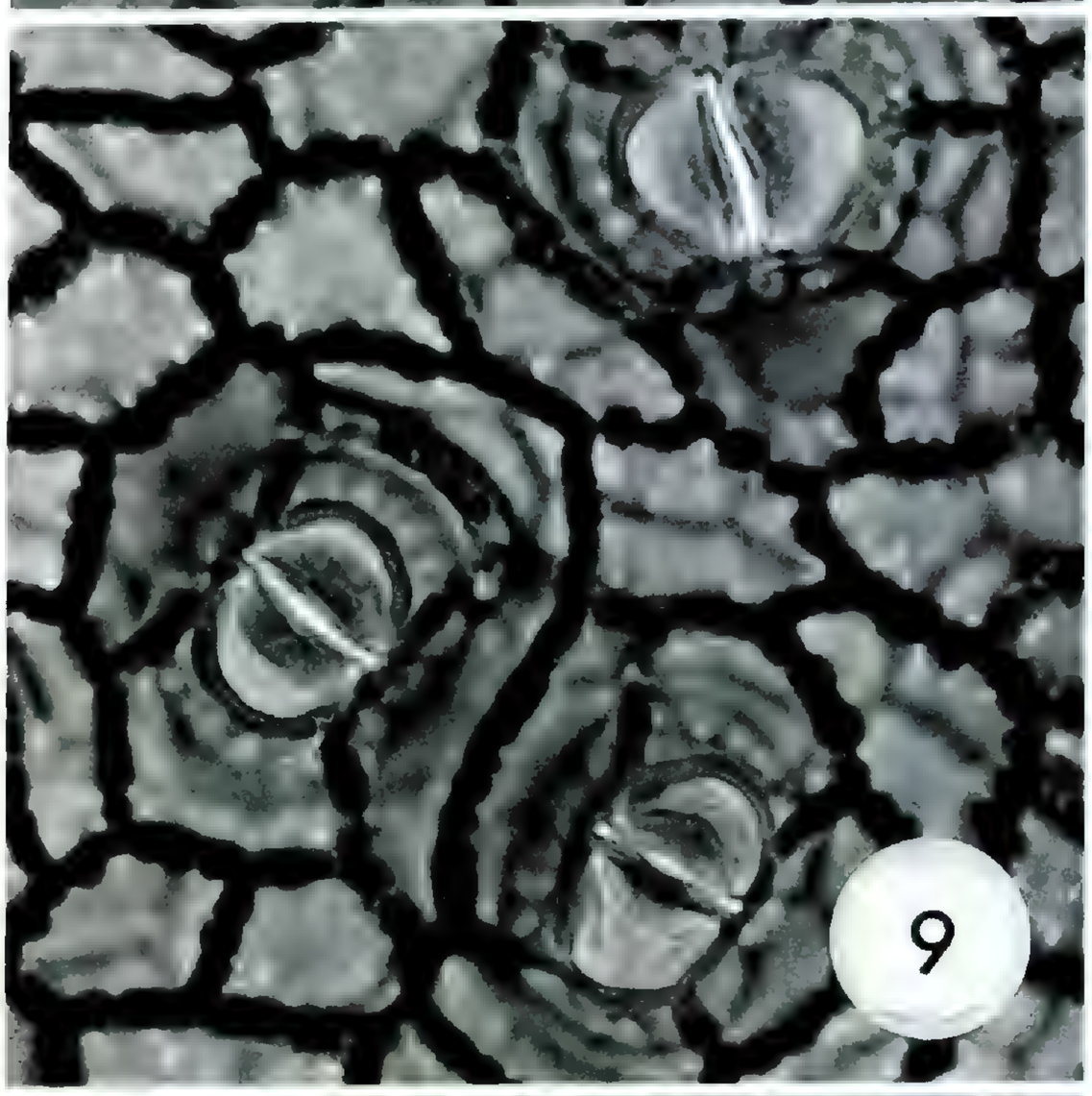
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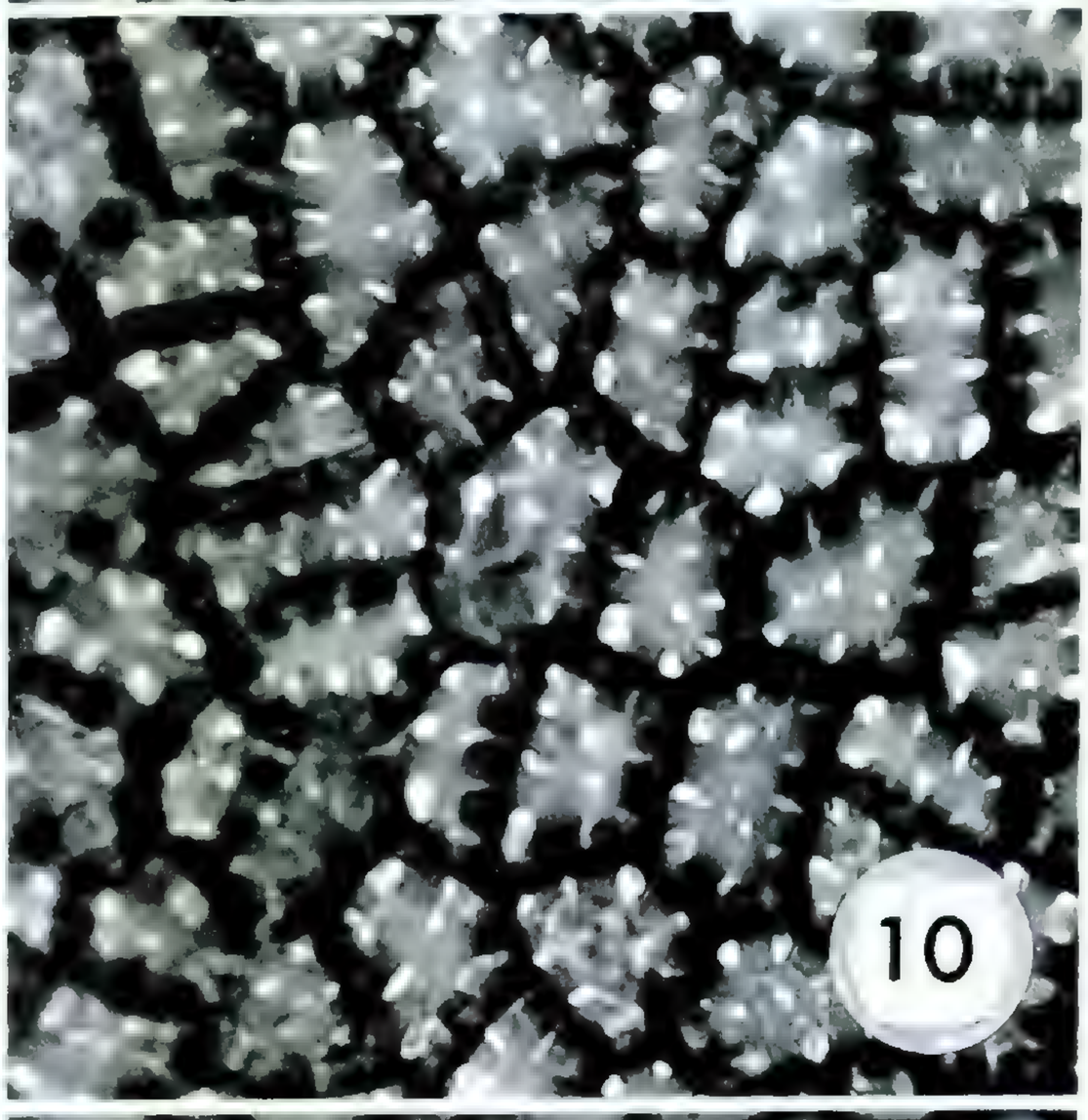
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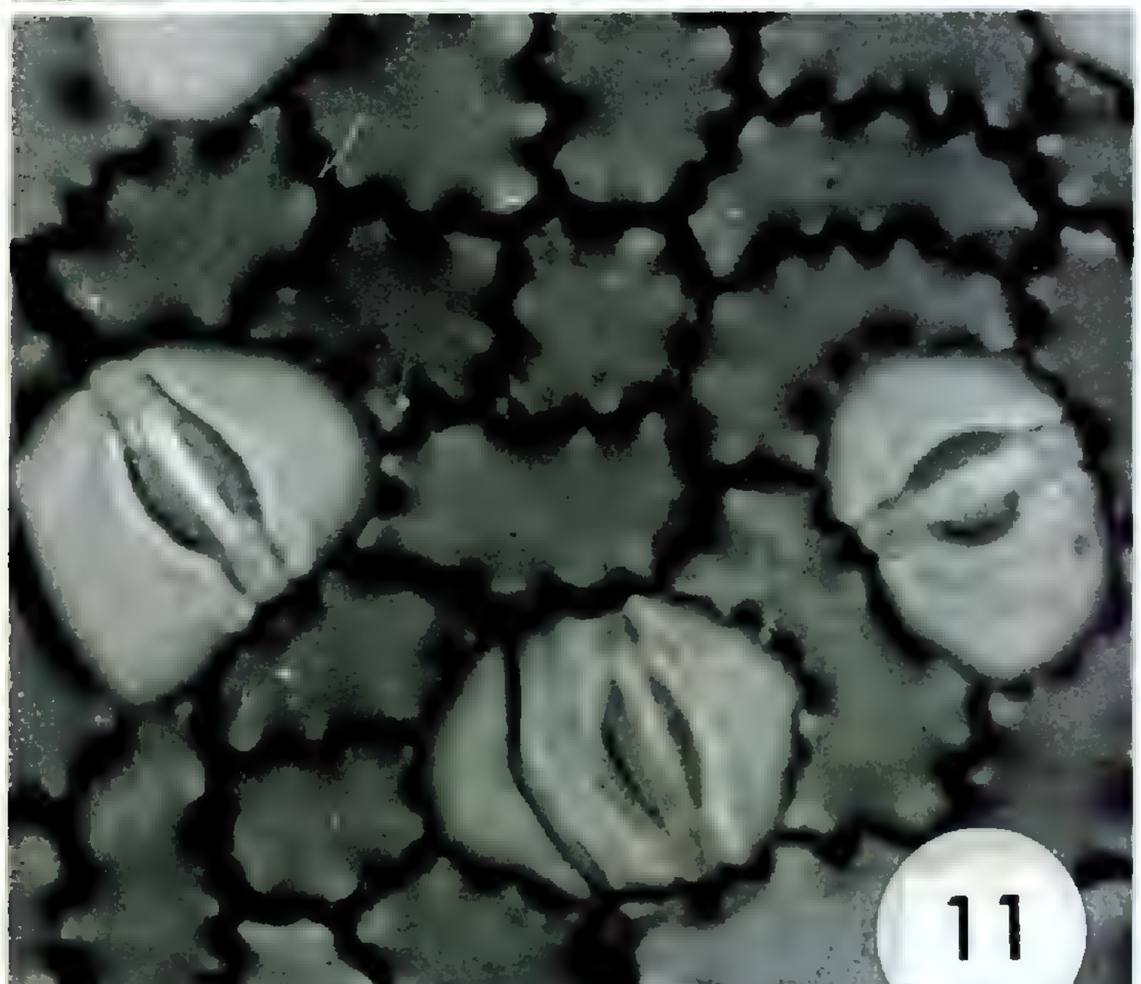
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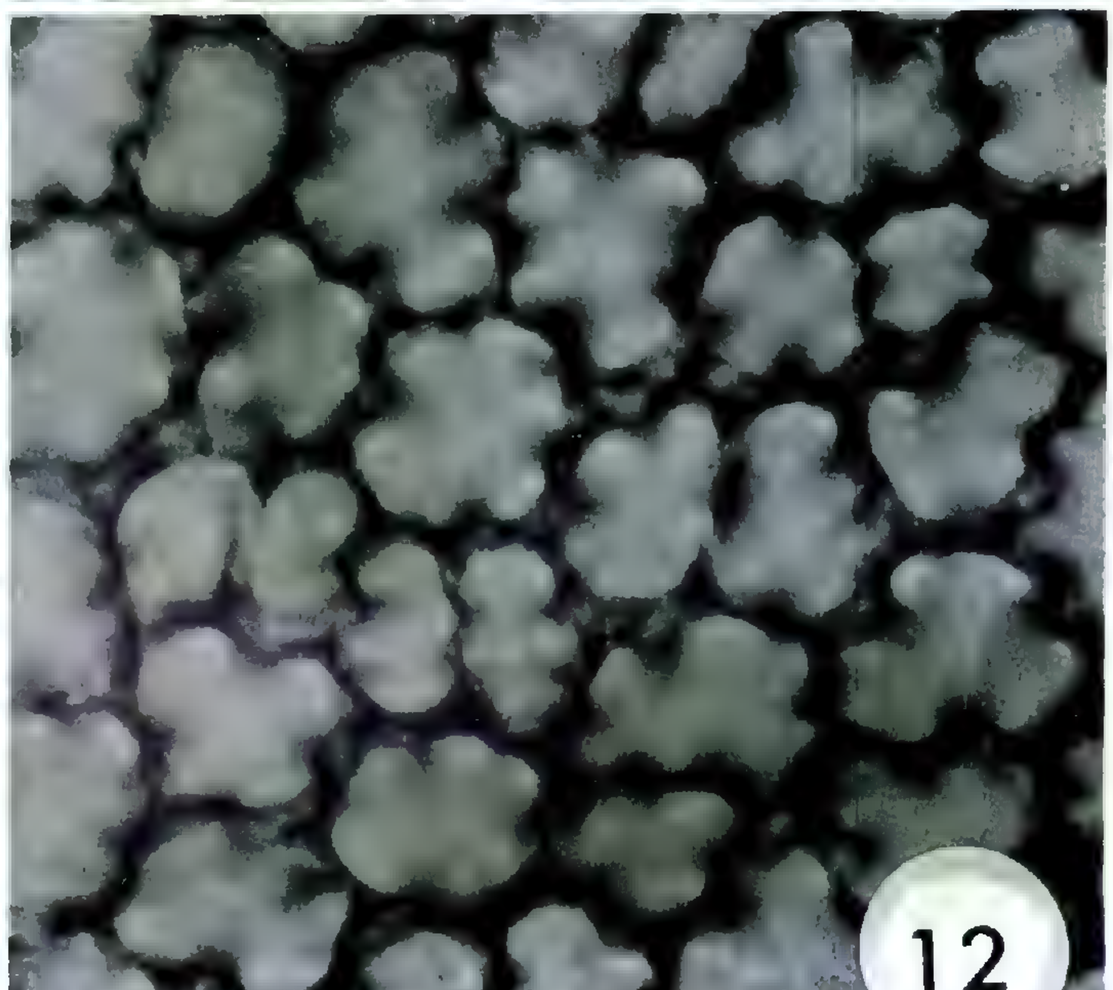
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and truly smooth, but, in practice, artifacts such as remains of epicuticular waxes, stain granules, and bits of adhering cell wall complicate such determinations. These difficulties could have been overcome by rigorous and prolonged chemical treatment, and by observation using SEM; however, one of the major purposes of this study is to develop a character set that is readily usable by general botanists and ecologists, and hence such highly specialized treatment was not employed.

Several separate features of the anticlinal walls can be characterized. The uniformity of thickness is one such character. Anticlinal walls can be regularly uneven (beaded, e.g., Figs. 7, 9), or if sinuous in outline can be thickened in the troughs (buttressed, e.g., Fig. 11), or can be irregularly thickened or smooth, which is the most common state. The straightness of the anticlinal walls is also important, and cuticles are scored for the majority of cells being angular (Fig. 13), regularly or irregularly rounded (Fig. 5), undulate (one trough and peak per wall, e.g., Fig. 18), or sinuous (more than one peak and trough per wall, e.g., Fig. 11). This anticlinal wall shape was placed in a seven category index by Wilkinson (1979), and this alternative method of scoring is also being tried for the global revision, to be followed by analysis to determine the better system. Uniformity of cell size and maximum dimension are also features being included. An example of between-species variation of average cell size can be seen in Figures 7 and 11. Of equal import is the variation apparent in some species in cell size and shape between the adaxial (upper) surface and the abaxial (lower) surface. Relative uniformity of features may be seen in Figures 7 and 8, while variation in shape between surfaces can be seen in Figures 11 and 12, and variation in cell size between surfaces may be seen in Figures 5 and 6.

While the number of subsidiary cells (2) in the Lauraceae and their arrangement (paracytic) are uniform across the family, and all species are hypostomatic, the stomatal complex still provides a rich character set, likely including many of the features that will prove critical in the delimitation of supraspecific taxa. As illustrated in transverse section in Figure 19, and as shown by Hill (1986) in his figure 1, the stomatal complex in the Lauraceae has sunken guard cells with over-arched subsidiary cells. Although the family is truly paracytic, to the non-specialist observing the cuticle in surface view the subsidiary cells appear to be guard cells, and the unspecialized cells in the adjacent row are considered to be subsidiary. Their variable arrangement leads to identifying the subsidiary pattern as virtually nonexistent, or anomocytic.

Possession of uneven-sized subsidiary cells (Fig. 9) has proven common only in certain genera, such as *Beilschmiedia*, and could be of taxonomic utility. By far the most variable feature of the complex, and hence possibly one of the most useful at various levels, is the nature of the two cuticular ledges (Fig. 19). The upper (Fig. 19 UL) protrudes upward and sometimes outward in the stomatal pore, and arises from the lateral walls of the subsidiary cells. In some taxa, the lower ledge (Fig. 19 LL) protrudes between the guard cells (Fig. 19 GC) and the subsidiary cells (Fig. 19 SC), sometimes forming into various shapes including those that look somewhat like butterflies (Figs. 20, 22). An additional taxonomic feature is added to this by the fact that these expanded ledges are variously deciduous.

Some genera, like *Endiandra*, have both ledges visible, although not expanded, and this "double" ledge can thus be used to distinguish this genus in Australia (Christophel & Rowett, in press). Some taxa, including many not found in Australia, have other ledge configurations, and in extreme cases (e.g., Fig. 24, *Aiouea guianensis* Aublet) the entire stomatal complex may be obscured by a thickened ring of cuticle. Finally, some features of cells adjacent to the stomatal complex may also be modified, such as the papillae in *Caryodaphnopsis* (Figs. 1, 3, 4).

The final category of taxonomically useful characters is derived from the presence/absence and features of various specialized cells. In the Lauraceae, all trichomes thus far reported in the litera-

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Figures 7–12. —7. Abaxial cuticle of *Beilschmiedia volckii* B. Hyland taken from L650, Botany Department Herbarium, Adelaide University from *B. Gray 3823* housed at QRS; collected in Australia.—8. Adaxial cuticle of *Beilschmiedia volckii*. All information and magnification as per Figure 7.—9. Abaxial cuticle of *Beilschmiedia elliptica* C. White & Francis from L643, Botany Department Herbarium, Adelaide University, from *B. Hyland 4128*, housed at QRS; collected in Australia; magnification as per Figure 7.—10. Adaxial cuticle of *Beilschmiedia elliptica*. All information and magnification as per Figure 7.—11. Abaxial cuticle of *Beilschmiedia obtusifolia* (F. Muell. ex Meissner) F. Muell. from L644, Botany Department Herbarium, Adelaide University, from *B. Gray 1279* housed at QRS; collected in Australia; magnification as per Figure 7.—12. Adaxial cuticle of *Beilschmiedia obtusifolia*. All information and magnification as per Figure 11.

20 µm
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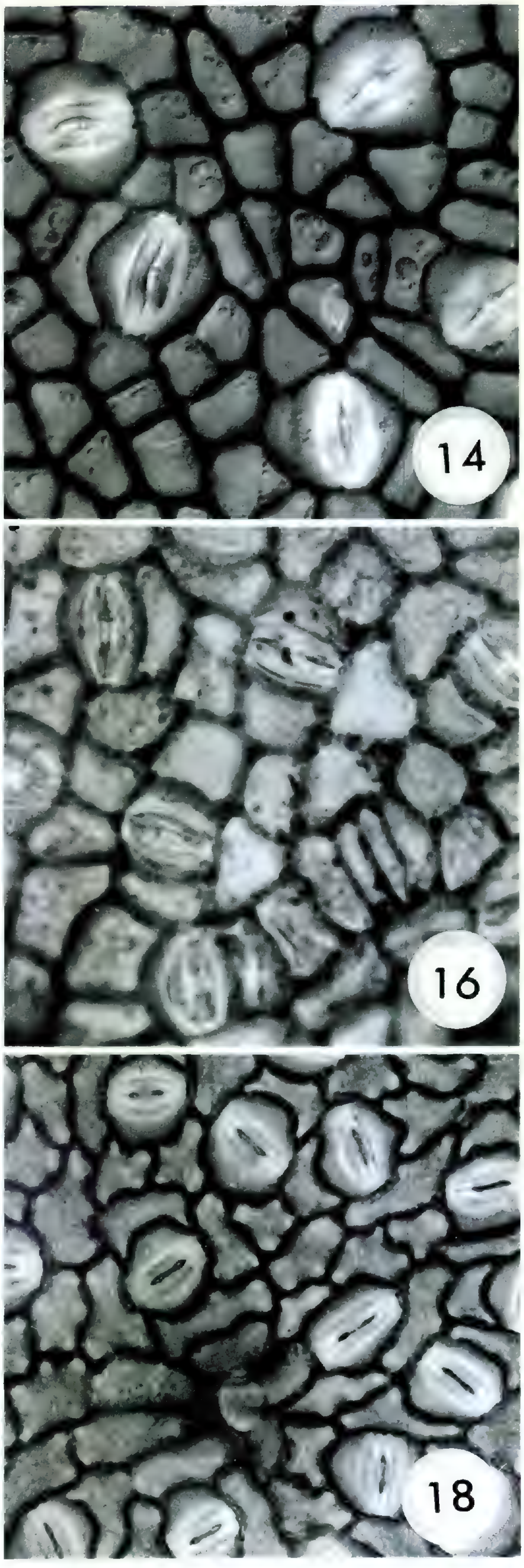
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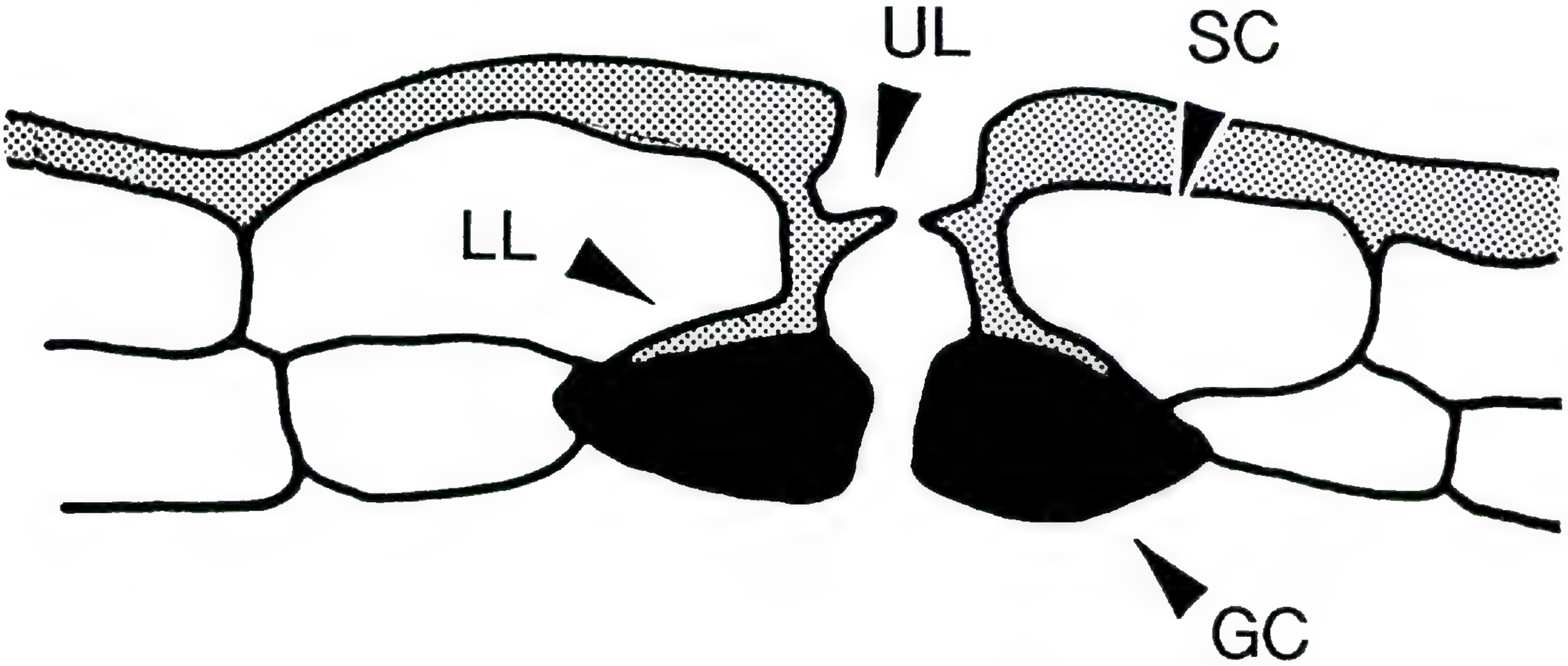

Figure 19. Diagram of transverse section of typical Lauraceae stomatal complex (modified from Hill, 1986, fig. 1). Stippled area shows actual cuticle, as would be seen in a cuticular preparation. Black area represents sunken, embedded guard cells (GC), over-arched by the subsidiary cells (SC). Upper cuticular ledge (UL) and lower cuticular ledge (LL), which vary in prominence across the family, are also shown. Leaf surface toward top in diagram.

ture or observed by the authors have been simple (e.g., *Litsea costalis*, (Nees) Kosterm. Fig. 13). Generally their bases can be characterized as poral, meaning that they consist not of a set of specially modified cells, but of a pore, or hole, at the junction of several non-stomatal cells. In some species, e.g., *Ocotea lentii* Burger, giant trichomes are found that clearly have rings of modified cells surrounding the trichome base. The trichome and its base provide separate suites of characters, as the trichomes are variously deciduous from species to species, and even in those species where they are not deciduous, they can be easily broken in preparation. Obvious features such as trichome density and trichome position relative to veins or areoles are also of potential taxonomic utility.

Some Lauraceae also display regions of thickened cells (5–20) that stain densely and are likely glandular. It should be noted that wound tissue has a similar appearance, but that interpretation can be discounted when the areas are regular in their location across a cuticle slice (and indeed duplicated on additional specimens). The final type of special epidermal structure that has been observed in the Lauraceae is the hydathode. Wilkinson (1979) suggested that structurally there are several types of hydathodes, but within this study the term is restricted to giant stomates. These structures are usually 2–2.5 times the size of normal stomates, and frequently occur over veins. It must be noted that some Lauraceae species have variable-sized stomates, and care must be taken to avoid labeling a large stomate at the extreme of a size range as being a hydathode.

Preliminary Results

When groups of related species or genera are examined for the expression of the above-described characters, some interesting preliminary results can be seen. For example, Christophel and Rowett (in press) noted that *Endiandra* species were charac-

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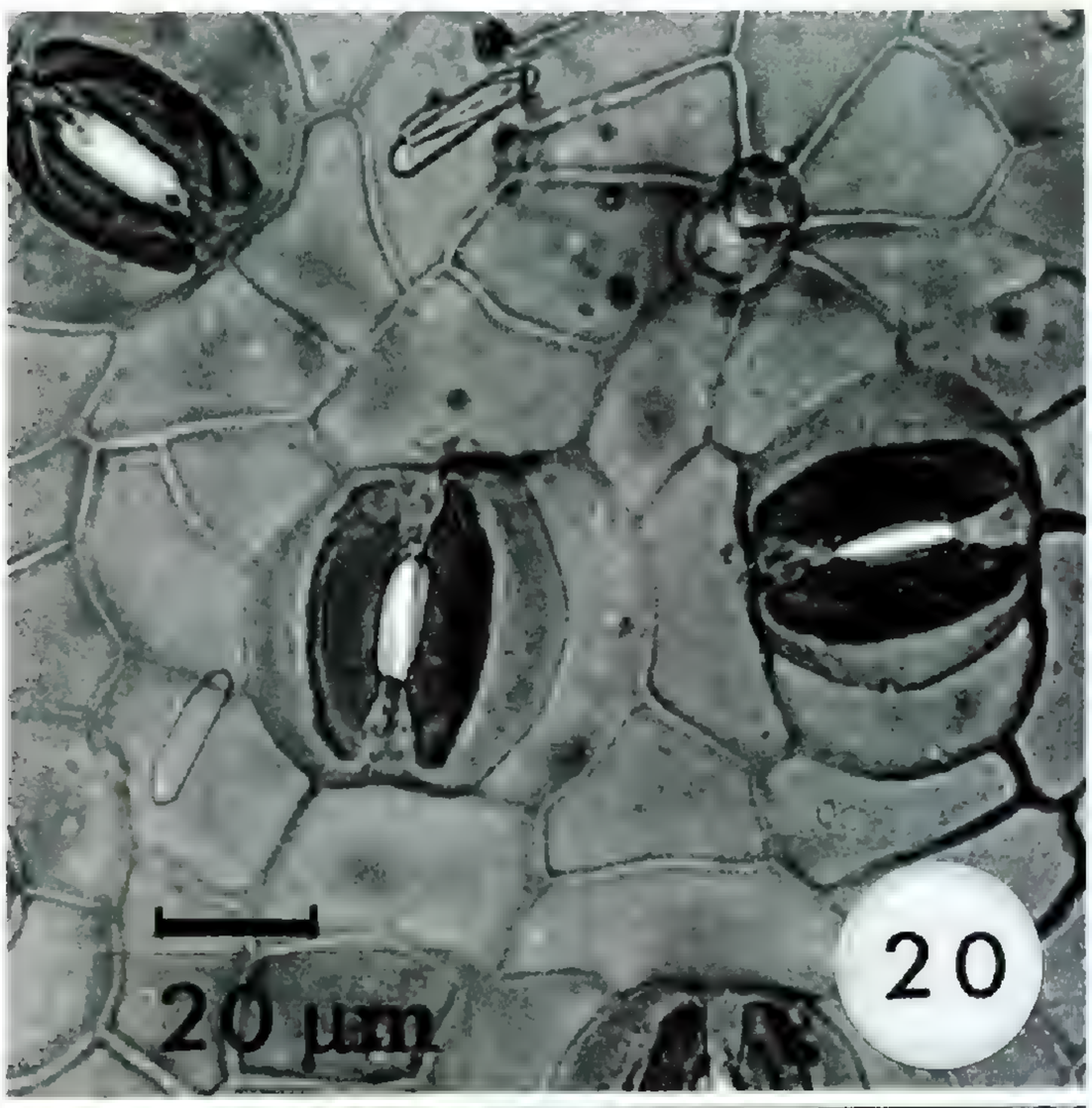
Figures 13–18. —13. Abaxial cuticle of *Litsea costalis* (Nees) Kosterm. Cuticle taken from L190, Botany Department Herbarium, Adelaide University from *B. Hyland 14130* housed at QRS; collected in Sembilan. Note dense simple hairs and poral hair bases.—14. Abaxial cuticle of *Endiandra montana* C. White taken from L691, Botany Department Herbarium, Adelaide University, from *B. Gray 2825* housed in QRS; collected in Australia; magnification as per Figure 13.—15. Abaxial cuticle of *Endiandra glauca* R. Br. Photographed with Nomarski interference contrast microscopy. Cuticle taken from L671, Botany Department Herbarium, Adelaide University from *B. Gray 3211* housed in QRS; collected in Australia; magnification as per Figure 13.—16. Abaxial cuticle of *Endiandra wolfii* B. Hyland. Taken from L705, Botany Department Herbarium, Adelaide University, from *B. Gray 1328* housed at QRS; collected in Australia; magnification as per Figure 13.—17. Abaxial cuticle of *Endiandra sieberi* Nees from L703, Botany Department Herbarium, Adelaide University, from *B. Gray 1504* housed at QRS; collected in Australia; magnification as per Figure 13.—18. Abaxial cuticle of *Endiandra kingiana* Gamble from L528, Botany Department Herbarium, Adelaide University, from *B. Hyland 14146* housed at QRS; collected in Sarawak; magnification as per Figure 13.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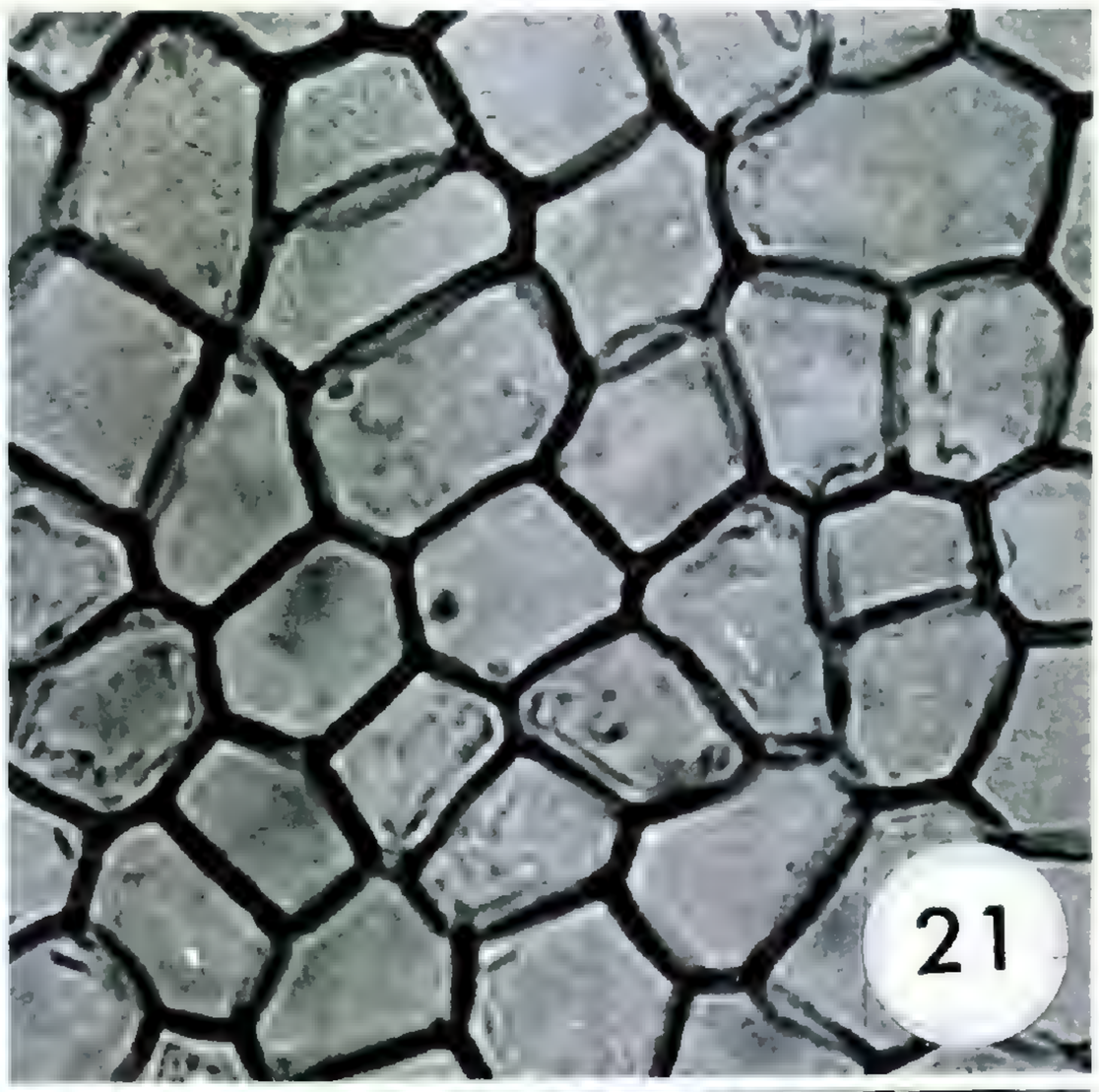
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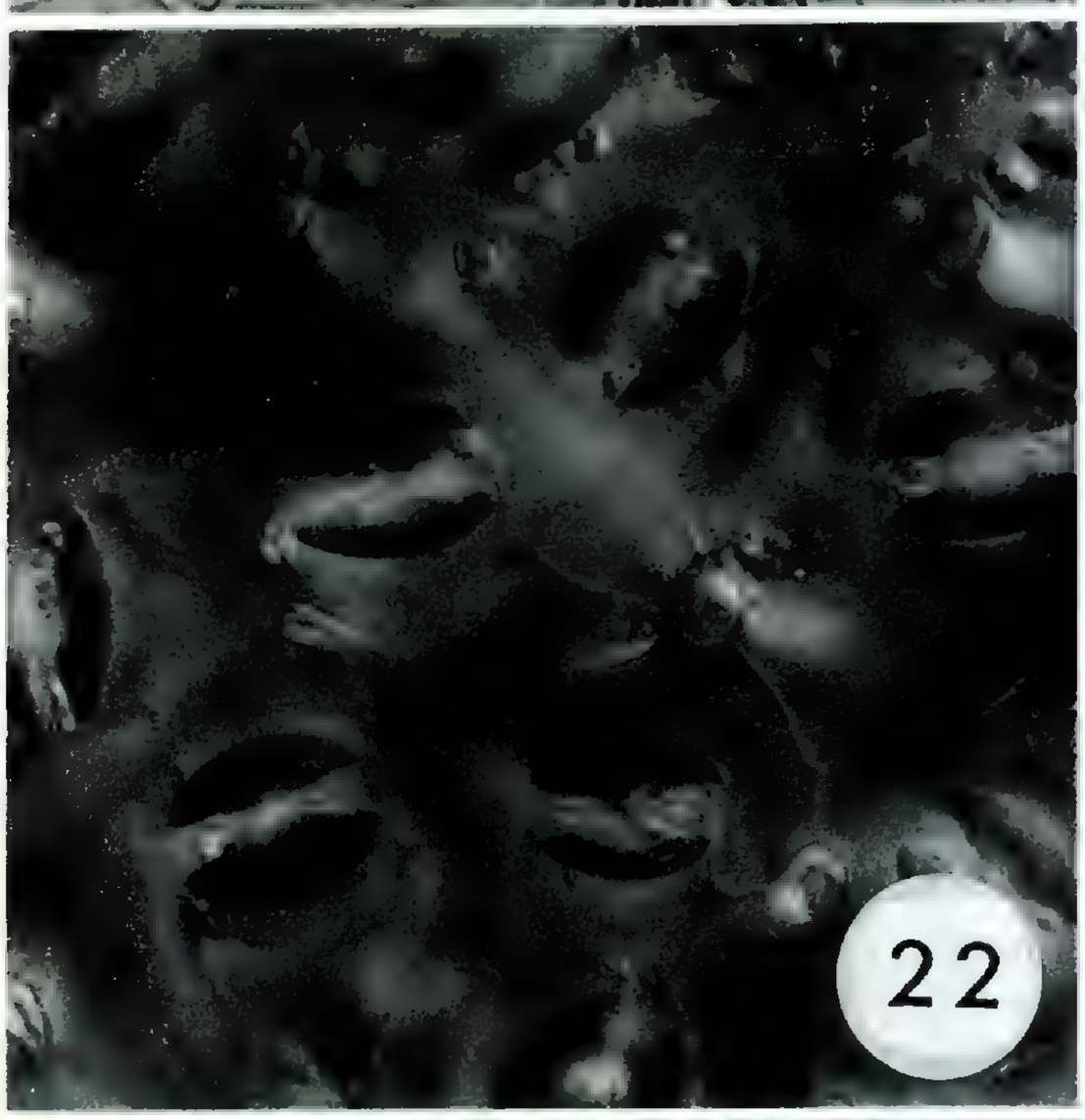
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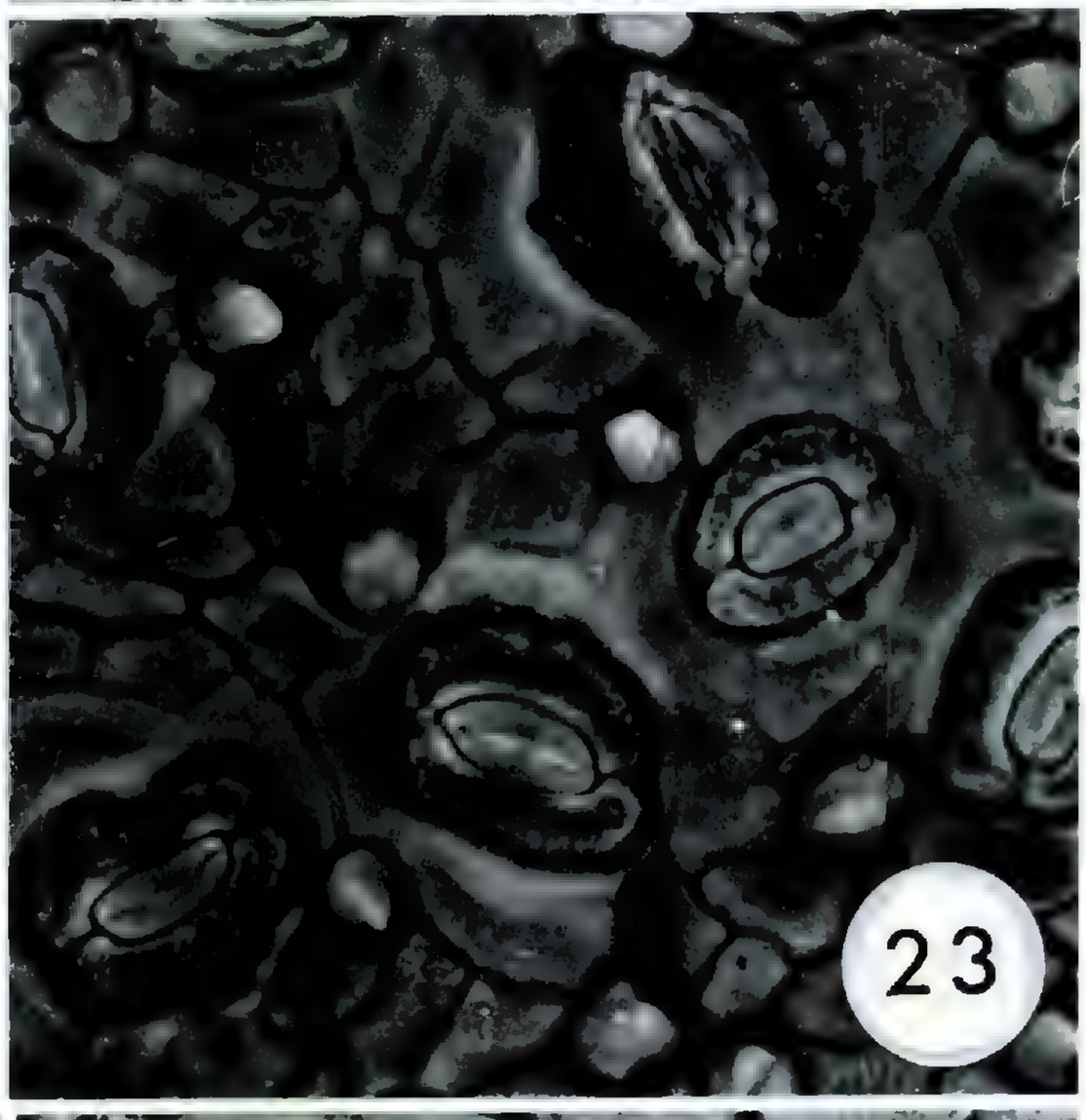
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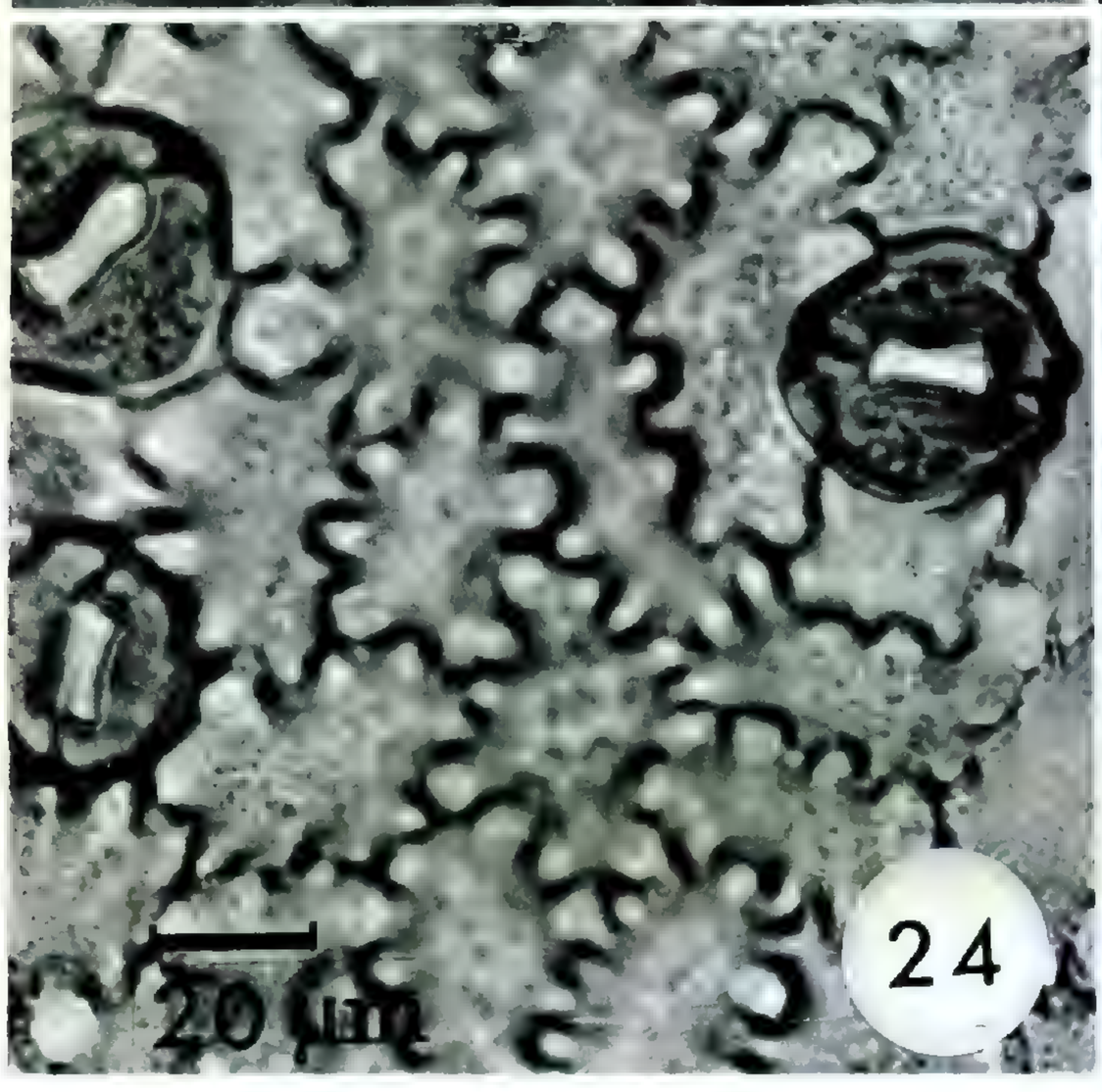
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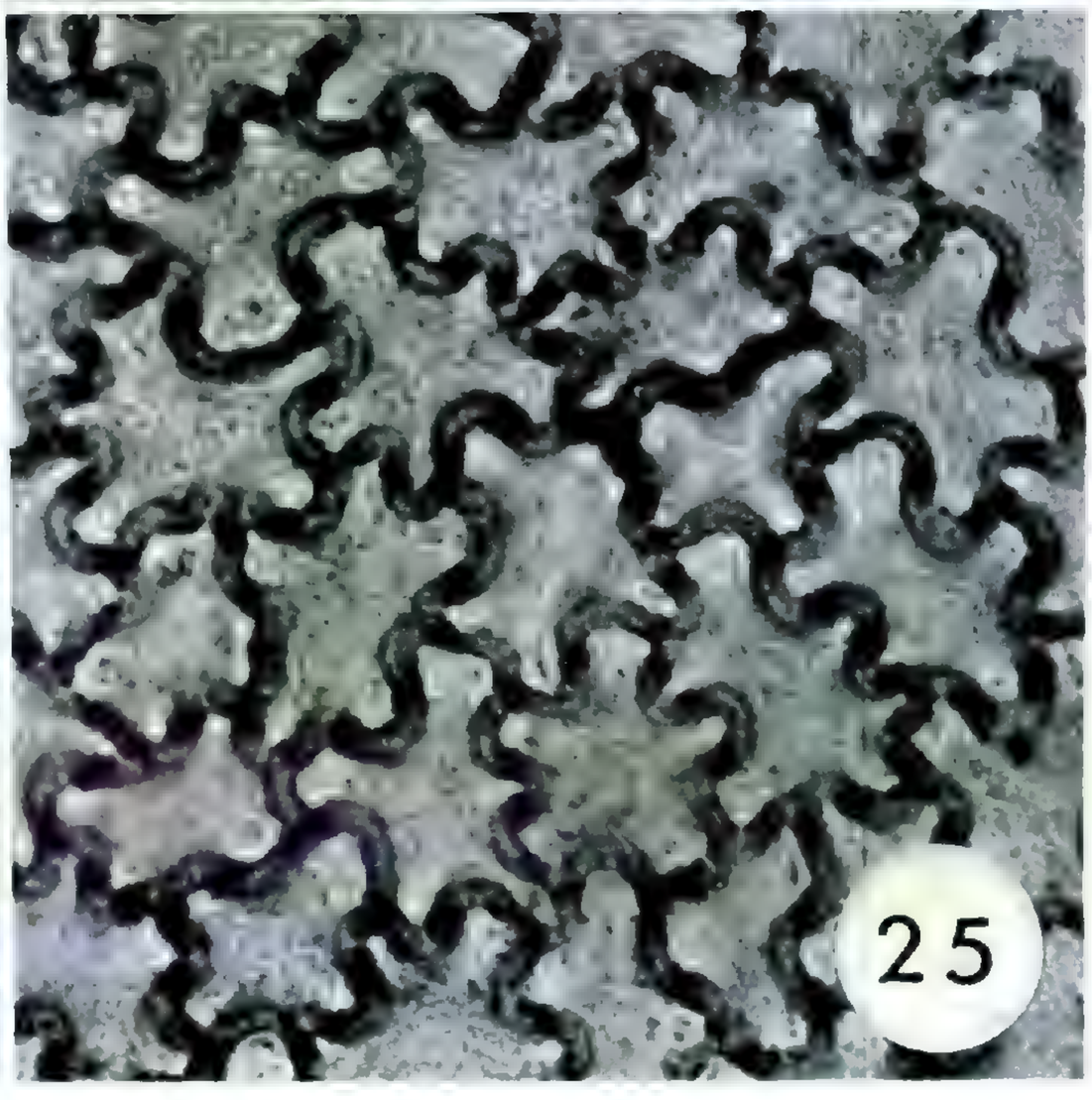
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terized in Australia by having relatively straight, thin, double stomatal ledges. These may be observed in Figures 14, 15, 16, and 17, where it can be seen that a thin, inner (upper) ledge is visible just inside the stomatal pore, and another parallel set of ledges (lower) can be seen outside of these, separated by approximately one-third of the subsidiary cell, and parallel to its long axis. While the other three Australian species illustrated (Figs. 14, 16, 17) are photographed with normal transmitted light, *Endiandra sieberi* Nees (Fig. 15) was photographed with interference contrast (Nomarski) microscopy, to compensate for unsatisfactory staining of that particular specimen. Not only does this clearly show the pairs of ledges, but the faint outlines suggest the position of the sunken guard cells may also be seen. *Beilschmiedia,* the sister genus to *Endiandra,* lacks these straight, double ledges. While straight, double ledges appear a good descriptor for *Endiandra,* it should be noted that other features are variable. For example, the anticlinal walls of *Endiandra montana* C. White, *E. wolfii* B. Hyland, and *E. glauca* R. Br. are straight, whereas *E. sieberi* Nees has irregularly rounded to undulate anticlinal walls.

A measure of the success of this character must be its effectiveness on extra-Australian species. To date 20 such species have been examined, and all show the double ledges. Some (e.g., *Endiandra kingiana* Gamble from Sarawak—Fig. 18) even illustrate the feature more clearly than the Australian species.

Beilschmiedia is considered to be closely related to *Endiandra* by most authorities (e.g., Hyland, 1989; Kostermans, 1957; Rohwer, 1993). In general, it can be separated easily by the fact that its species normally possess nine fertile anthers. However, just as in *Endiandra,* in Australia a group of *Beilschmiedia* species (4) possess only six anthers. While this would qualify them for membership in Allen's *Brassiodendron,* Hyland (1989) has placed them in *Beilschmiedia* based on a suite of other features.

Christophel and Rowett (in press) were able to separate *Endiandra* and *Beilschmiedia* in Australia quite easily in that no species of *Beilschmiedia* had the nearly straight, double ledge that *Endiandra* stomates possess. *Beilschmiedia* itself is characterized by all species having some degree of uneven anticlinal wall thickening (buttressing or beading) (Figs. 7, 9, 11). Some species, such as *Beilschmiedia obtusifolia* (F. Muell. ex Meissner) F. Muell. (Figs. 11, 12), show a marked degree of difference in the degree of thickening between the adaxial and abaxial walls. This feature, however, is not restricted to *Beilschmiedia,* as some *Endiandra* species show anticlinal wall thickening.

In addition, all Australian species appear to have some degree of unevenness in the size of the two subsidiary cells (e.g., *Beilschmiedia elliptica* C. White & Francis, Fig. 8). This is not as reliable a feature for generalized identification, however, as in many species it is not visible on stomates in some regions; hence a random leaf piece might not show them.

Cuticular analysis can also be used on species groups, with potential biogeographical significance. One of the most obvious disjunctions in the family occurs in *Caryodaphnopsis,* which has species recorded from South America and also from Southeast Asia. Examination of the cuticles of *Caryodaphnopsis* species shows not only some unique features, but also highlights the fact that both geographic groups possess them. While the adaxial (upper) cuticular surface of *Caryodaphnopsis* species usually has smooth to granular periclinal walls (Fig. 2), the abaxial surface invariably has papillae present to some extent on the periclinal walls. The density of the papillae varies from species to species, but in all species examined papillae are clearly present on the cells surrounding the stomatal complex, and even over-arch it to a degree. This feature can be

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Figures 20–25. —20. Abaxial cuticular surface of *Rhodostemonodaphne grandis* (Mez) Rohwer showing butterfly-shaped lower cuticular ledge (dark stained). Cuticle from specimen L104, Botany Department Herbarium, Adelaide University, from *Mori 20904* at MO; collected in French Guiana.—21. Adaxial cuticular surface of *Rhodostemonodaphne grandis.* Specimen citation and scale bar as per Figure 20.—22. Abaxial cuticular surface of *Rhodostemonodaphne kunthiana* (Nees) Rohwer showing butterfly-shaped lower cuticular ledges. Photographed with Nomarski interference contrast microscopy; prepared from L106, Botany Department Herbarium, Adelaide University. Originally from *Zak 4452* at MO; collected in Ecuador; magnification as per Figure 20.—23. Abaxial cuticle of *Cinnamomum sellovianum* (Nees & Mart.) Kosterm. showing cuticular collar surrounding stomatal apparatus; taken from L124, Botany Department Herbarium of Adelaide University. Prepared from *Harley 25261* at MO; collected in Brazil; magnification as per Figure 20.—24. Abaxial cuticle of *Aiouea guianensis* Aublet from L113, Botany Department Herbarium, Adelaide University, from *Jensen Jacobs 1986* at MO; collected in Guyana.—25. Adaxial cuticle of *Aiouea guianensis.* All information and magnification as per Figure 24.

seen in the three species illustrated for this paper (Figs. 1, 3, 4); two of these (*Caryodaphnopis henrii* A. Shaw and *C. tonkinense* (Lec.) A. Shaw) were collected in China and the third, an as-yet-undescribed species, occurs in Peru.

Discussion

The use of cuticular features for various taxonomic delimitations has been successful in various diverse groups (e.g., Araucariaceae—Stockey & Ko, 1986; Myrtaceae—Christophel & Lys, 1986). It has also proven satisfactory for family identification (Hill, 1986) and local generic differentiation (Ow et al., 1992) within the Lauraceae. Preliminary investigations have now shown in this paper that, based on genera such as *Endiandra, Beilschmiedia,* and *Caryodaphnopsis,* the use of a suite of cuticular characters applied to a global range of genera and species has great promise.

Concerning the examination of *Endiandra,* of particular interest among the Australian species are the two that have six anthers (all other species in the genus possess three anthers). Hyland (1989) commented on them and noted that while some workers (e.g., Allen, 1942) placed them in a separate genus, *Brassiodendron,* he (Hyland) considered anther number by itself to be a non-definitive character, and included the two species in *Endiandra* based on a majority of other features. *Endiandra montana* C. White (Fig. 14) is one of those six-anthered species, and is shown to clearly belong with the other *Endiandra* species because of the double ledge cuticle feature. The other six-anthered species, while not illustrated here, also has the double ledge, and hence supports Hyland's placement in *Endiandra.* It should be noted that no attempt is made here to infer that the double ledge character is more taxonomically important than anther number, but it does support Hyland's placement of those species in *Endiandra,* which was based on a suite of morphological characters.

The four species of *Beilschmiedia* in Australia that possess six anthers have been examined, and show no obvious differences from the remaining species in the genus. This can be seen by comparing one of those four, *Beilschmiedia volckii* B. Hyland (Figs. 7, 8), to the nine-anthered species *Beilschmiedia obtusifolia* (F. Muell. ex Meissner) F. Muell. and *B. elliptica* C. White & Francis (Figs. 9, 10, 11, 12). Perhaps of even more significance is the fact that they are clearly distinct from the six-anthered species of *Endiandra* in their stomatal ledge structure. The few species of extra-Australian *Beilschmiedia* examined thus far have agreed with the features found by Christophel and Rowett (1995) for that genus in Australia.

Following from the results of the study of *Caryodaphnopsis* cuticles, it should be noted that in the Lauraceae, papillae are not restricted to that genus. For example, they can be found in a few species of *Beilschmiedia* and are reported to be common in *Aniba* (Kubitzki & Renner, 1982). However, it is the similarity of the structure of the papillae, and not only their presence, that supports the placement of these disjunct species of *Caryodaphnopsis* in the single genus.

The exclusive use of cuticle characters within the family is not without some problems, or at least challenges, however. Christophel and Rowett (in press) have shown that within Australian species of *Cryptocarya,* good generic delimiting features are not obvious. Examination of approximately 20 additional species from this genus occurring outside of Australia has not solved this difficulty, although it has become clear that the decision to sink *Ravensara* from Madagascar into *Cryptocarya* s.l. is a good one, based on epidermal similarities.

Another group that should prove challenging is *Cinnamomum.* It can be seen that South American species of this genus have distinctive cuticular signatures (Fig. 23) and that they are clearly different from the *Cinnamomum* species of Australia figured by Christophel and Rowett (in press). Interestingly, the American *Cinnamomum* species had been placed until recently in *Phoebe* (Rohwer, 1993). Asian species of the genus, including the type species, form a third distinctive group, and further study may well lead to the conclusion that the group is not natural (and is perhaps polyphyletic) as it is currently defined.

The tripli-nerved, or acrodromous venation pattern is common in both *Crypotcarya* and *Cinnamomum.* However, no positive correlation has been found between groups of species possessing that character and those sharing common cuticular features. Basic venation characters are nonetheless being initially included in the global revision in order to test them on the full spectrum of species in the family.

Hyland (1989) suggested that the generic complex of *Litsea, Neolitsea,* and *Lindera* is also in need of further detailed study. Christophel and Rowett (in press) had little difficulty separating the three genera based entirely on Australian material, but those species represent only a small proportion of the total for the three genera, and the lack of single outstanding features to separate them, similar to the double ledges of *Endiandra,* suggests that the group could provide a challenge on a global level.

Finally, some of the largest genera (e.g., *Ocotea* and *Nectandra*) occur in South America, and that material has been the least thoroughly studied by us to date. A strong possibility exists that both of these genera are currently unnatural (H. van der Werff, MO, pers. comm.) and hence much work needs to be done here. Preliminary observations on material from various genera in South America, however, suggest that some features that are highly diagnostic in Australian material (e.g., the butterfly-shaped cuticular ledges prominent in *Cryptocarya* and to a lesser extent, *Cinnamomum*) are in fact widespread in other geographic regions and in other currently prescribed taxa. The potential utility of such characters will only be assessable once thorough studies of the material have been made.

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Experimental and Molecular Approaches to Plant Biosystematics

The proceedings of the Fifth International Symposium of the International Organization of Plant Biosystematists (IOPB)

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Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin.*" Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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Cover illustration. *Pavetta camerounensis* subsp. *camerounensis* S. D. Manning, sp. nov., by Linda Ellis.

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ALWYN HOWARD GENTRY, 1945–1993: A TRIBUTE

This issue of the *Annals of the Missouri Botanical Garden* is dedicated to the memory of Alwyn H. Gentry. The first section contains contributions by some of those scientists who knew him. It begins with an overview of his life by James S. Miller, including lists of Gentry's publications and of his students. A transcript of the presentations given at the memorial service held at the Missouri Botanical Garden on 20 August, 1993, follows. The speakers were: Theodore M. Barkley, Hugh H. Iltis, Walter H. Lewis, Enrique Forero, Mark Plotkin, Oliver Phillips, and Ricardo Rueda. The tribute closes with the eulogy delivered by Peter H. Raven.

Ann. Missouri Bot. Gard. 83: 433–460. 1996.

ALWYN HOWARD GENTRY, 1945–1993

Al Gentry with flowering branch of *Tabebuia* in Costa Rica. The Central American species of *Tabebuia* were the subject of his Master's Thesis, and Costa Rica was the first tropical country that he visited.

The Life and Work of Al Gentry

On August 3, 1993, a small airplane on a Conservation International research mission crashed into an isolated mountain ridge in western Ecuador, near Guayaquil. Alwyn H. Gentry and Theodore A. Parker III, arguably the leading authorities on the botany and ornithology of tropical America, died in the crash along with the pilot and Eduardo Aspiazu, an Ecuadorian ecologist and President of the Guayaquil chapter of Fundación Natura. Three other researchers survived the crash. This event prematurely ended the career of one of the greatest plant explorers and botanists of all time. Gentry's knowledge of neotropical plants was unsurpassed, and Parker's extensive experience with Latin American birds mirrored Gentry's knowledge of its plants. Anyone familiar with Gentry knew that he worked tirelessly, was ambitious, conducted ground breaking and insightful scientific studies at a tremendous rate, and was passionate in his quest for understanding and conservation of the most diverse natural areas in the world.

Al Gentry was born on January 6, 1945, in Clay Center, Kansas. He graduated from Clay County Community High School in 1963, where he was both valedictorian and outstanding science student, and he began his university studies at Kansas State University in the fall of that year. He graduated in 1967 with two degrees, one a bachelor of arts in physical science and the other a bachelor of science in botany and zoology.

He spent the summer of 1967 in Costa Rica, his first immersion in the tropics, on an Organization of Tropical Studies (OTS) Introductory Course. Here he began his work on Bignoniaceae, which was to remain his primary monographic interest for life. In the fall, Gentry moved to Madison, Wisconsin, to begin his master's studies in the botany department with Professor Hugh H. Iltis. He spent the summer of 1968 at the University of Miami in a seminar on tropical botany, finished his thesis on *Tabebuia* (Bignoniaceae) in Central America in the fall semester, and graduated with an M.S. degree in January of 1969. With support from the Davis Fund of the University of Wisconsin, he left immediately for fieldwork in Costa Rica, Panama, and Mexico from January to March.

In the fall of 1969, Al began his doctoral studies at Washington University in St. Louis, Missouri, under the direction of Professor Walter Lewis. With support from a National Science Foundation pre-doctoral dissertation improvement grant, Gentry left for field studies in Costa Rica and Panama in May of 1971. He returned to Panama in August, working for a year as curator of the Summit Herbarium, a position managed on a one-year rotation basis by the Missouri Botanical Garden and generally filled by graduate students working on the systematics of Central American plants. His Ph.D. thesis, completed for graduation in December of 1972, was entitled "An Eco-evolutionary Study of the Bignoniaceae of Southern Central America."

In October 1972, Gentry was hired as an Assistant Curator by the Missouri Botanical Garden, where he spent his entire career. In 1974 he made his first trips to South America, South Africa, and Madagascar, and late in the year he made his first trip to Peru, the country that would remain the major geographical focus of his studies.

During his career at the Missouri Botanical Garden, Gentry's interests in systematics and ecology continually expanded to include a wide variety of topics, but most of his time and energy focused on three: the systematics of Bignoniaceae; tropical floristics, particularly the flora of Peru; and studies of the correlation between environmental variables and patterns of forest diversity and composition.

Gentry became interested in the systematics of Bignoniaceae during his first trip to the tropics on the OTS course in Costa Rica in 1967. Although he was initially attracted to the brilliant-flowered genus *Tabebuia* and chose it as the subject of his master's studies, his interest rapidly shifted to the vining genera that comprise the majority of the species. Throughout his life he maintained interest in the family, and he continued to publish profusely on it. His graduate studies led to his first ten publications on Bignoniaceae, and he published the first part of a *Flora Neotropica* treatment of the family in 1980 and the second in 1992. In addition, he contributed treatments of the family for nine floristic volumes and had five treatments of the family in press at the time of his death. His interest in the family was not solely concerned with alpha taxonomy, however. He authored and coauthored studies on the ethnobotany, palynology, cytology, and chemistry of the family, and even as early as his doctoral studies he began investigating pollination mechanisms and the ecological importance of the family.

At the time that Gentry joined the Missouri Botanical Garden's research staff, the group was deeply committed to completion of the *Flora of Panama*, an ongoing project that had begun with fieldwork in the 1920s and had been appearing as fascicles in the *Annals of the Missouri Botanical Garden* for nearly three decades. The 1970s at the Garden marked a decided effort to bring the project to completion, and Gentry played a major role, contributing the *Flora of Panama* treatments for Bignoniaceae, Buxaceae, Humiriaceae, Rafflesiaceae, and Sabiaceae. He also made a significant contribution by routinely identify-

Figure 1. Gentry in Peru with Camilo Díaz and Rosa Ortiz de Gentry.

ing the steady stream of incoming collections, and he published notes and new species in eight additional families. This had a variety of affects on Gentry. First, it was the beginning of the development of what were to become unequaled skills in general plant identification. Second, he began his studies of the other plant groups, such as Sabiaceae, Buxaceae, and Passifloraceae, that continued to remain secondary interests in later years. He also became adept at assembling floristic information and acquiring the basic skills that later enabled him to coauthor two florulas in Ecuador, Río Palenque with C. H. Dodson, and Jauneche with C. H. Dodson and F. M. Valverde, and one of the Chocó, Colombia, with Enrique Forero.

However, it was Peru that ultimately became Gentry's primary floristic focus. After his first trip in 1974, he returned there in 1976 and at least once a year for every year until his death, making 33 trips. He published extensively on the Peruvian flora and developed collaborative relationships with many of his Peruvian colleagues, particularly Rodolfo Vasquez and Camilo Díaz.

Gentry became famous for his use of transect samples to assess vegetation. He collected his first transects as part of his OTS training in 1967, probably with little more in mind than comparing two adjacent vegetation types, but perhaps his greatest research arose from this auspicious start. As part of his doctoral studies, Gentry laid out transects at Madden Lake, Pipeline Road, and Curundu in Panama, this time to document the importance of Bignoniaceae as the major liana family in tropical forests and to study species phenology and pollination. It was not until later that he began to view the transects as a tool that allowed a relatively quick method of measuring diversity, taxonomic composition, and structure of forests.

Up until he began his studies, no one had ever collected a data set with any geographically significant coverage. Most of the ecological sampling that had been done used a variety of different methods and was thus not comparable from site to site. Gentry's brilliance was to devise a method that allowed a representative sample to be captured in a brief period of several days. This, coupled with his ever-increasing ability to identify tropical plants, particularly from vegetative characters, allowed him to amass a data set that, while with some limitations and assumptions, was comparable from site to site. Of course, another important character was that Gentry simply knew no limits. There are few people who would embark on explaining patterns of diversity and taxonomic composition of forests on a worldwide basis expecting to collect all of their own data. Gentry, trained as a taxonomist, took on an ecological problem that had been beyond the imagination of the ecological research community.

The method involved sampling all of the woody species greater than 2.5 cm diameter at breast height (DBH) in one-tenth of a hectare. He stretched a 50-m line through the forest and sampled all plants within one meter of either side. This he repeated ten times, and the sum of ten 2 × 50-m transects totaled 0.1 ha. With his knowledge of tropical plants, Gentry could rapidly make decisions about how many individuals encountered represented new species. Anything questionable was vouchered for later study in the herbarium, and each species was vouchered at least once. The final analysis could only be completed after all of the specimens had been identified. Thus even in the richest forests, he could collect the site in a week, and with another week in the herbarium, complete his analysis.

The vast majority of plants encountered at a given time in any forest that Al censused were sterile. Identifying them thus required either the effort of multiple visits to a given site to obtain the majority of species in fertile condition or the ability to accurately identify sterile specimens. Gentry's bold determination led him to the second option; this required that he develop and refine the capacity to work with sterile specimens. For years he carried a notebook with a draft key to families and genera of neotropical genera based on vegetative characters, and as he encountered new taxa he continually revised his text. This effort led to Gentry's remarkable capacity to identify neotropical plants from all sorts of specimens, and to the publication of his *Field Guide to the Families and Genera of Woody Plants of Northwest South America.*

Gentry's contributions to science were phenomenal. His more than 200 published works, with many additional articles still in press, cover a wide variety of subjects. He radically changed our modern concepts of the classification of Bignoniaceae and contributed to our knowledge of many other families as well. The publications resulting from the data that Gentry and his colleagues collected from 226 different 0.1-ha transects revolutionized the study of patterns of plant diversity. The transect studies that Gentry began as a graduate student expanded to more than 200 sites worldwide, and the focus of the studies shifted from attempting to study the importance and phenology of Bignoniaceae to attempting to understand patterns of plant diversity and the taxonomic composition of forests.

At the same time that he amassed such an impressive publication record, however, he also had an enormous impact as an explorer, plant collector, and teacher.

Gentry as Explorer/Plant Collector. Gentry made more than 80,000 plant collections, and hundreds of new species have been based on these specimens. Many were collected in the course of ground-breaking expeditions to remote regions of tropical America, some of them never before visited by botanists. Gentry's stamina and enthusiasm on these expeditions, as well as his near obliviousness to physical discomfort, were legendary. On one occasion (recounted in *A Parrot Without a Name,* by Stap, 1990), Al and Camilo Díaz became lost for over three days in a remote location in the Peruvian Amazon, finally re-emerging back at camp haggard and disheveled. Despite having wandered without food or shelter (they survived on nuts, snails, and, finally, palm heart, retrieved from a tree Al cut down with his jacknife), Al paused only long enough for a brief meal before resuming collecting, protesting over the objections of fellow expedition members that now he would have to work extra hard to make up for the time lost. Even those who worked with him under more mundane circumstances can attest to his tireless persistence, having suffered through late nights of pressing plant specimens amassed during long and strenuous days of collecting. But that tirelessness was a reflection of Gentry's belief in the fundamental importance, even urgency, of understanding tropical forests. How could one rest when there were so many marvels to be uncovered, so many undescribed species, so many vanishing before they could even be described?

Gentry as Teacher. Despite his notoriously frenetic schedule, Gentry found time—and indeed, considered it his mission—to encourage and instruct promising young botanists. Over the course of his career, he supervised the theses of about 20 students. At the time of his death, he was supervising nine graduate students, and many more had applied or were planning to apply to graduate schools in St. Louis, specifically so they could work with Gentry. Many of these were from the tropical countries he so loved. Perhaps one of Gentry's greatest legacies is his inspiring and launching the careers of a cadre of the next generation of tropical biologists (see list of students following publications).

At the time of his death, Al Gentry was involved in a myriad of projects. His monographic work on neotropical Bignoniaceae had continued, although the manuscripts had not yet been written, and he was well into a study of Malagasy members of the family. The database that he had developed contained records for some 55,000 herbarium collections he had examined from more than 122 herbaria around the world. William G. D'Arcy has assumed primary responsibility for the completion of Gentry's studies of Bignoniaceae, and Warren D. Hauk has joined the Garden staff to help with this task. This work will include completion of revisions for those genera that were not treated in the two volumes of Bignoniaceae Gentry contributed

to the *Flora Neotropica.* Gentry had envisioned two additional volumes for treatment of the family. He also left an unpublished manuscript treating the Bignoniaceae of Colombia, which will be published in the *Flora de Colombia* series. During his career Gentry assembled the world's richest herbarium collection of Bignoniaceae, including his own collections and those he received as gifts from other institutions. These collections and his database are readily available; the Missouri Botanical Garden encourages other researchers to study and use these resources. A "Gentry Invitation Series" has been established for taxonomic publications by people who are relying heavily on material left by Gentry or who wish to pay tribute to the contributions he made to their work. Those interested should contact W. G. D'Arcy at the Missouri Botanical Garden.

The transects occupied an ever increasing percentage of Gentry's time and were undoubtedly the part of his work he planned to focus most on in the future. In 1990, the Rapid Assessment Program (RAP) Team was founded at Conservation International, and Gentry began working half-time with Louise Emmons, Robin Foster, and Ted Parker to conduct quick inventories of areas deemed to be of great conservation significance. Gentry's 0.1-ha transects fit the RAP Team philosophy perfectly, and his participation helped serve his need for even more opportunities to install transects and collect data from an ever increasing number of sites.

Al Gentry certainly never imagined that the data that he and his collaborators had amassed from 226 0.1-ha transects were, in fact, ready to be summarized. At the time of his death, data from only about 90 of his sites had been computerized, and these were in drastic need of revision to include names of newly identified plant specimens. Gentry generally worked from hand-calculated summaries of each site. Due to advances in software over the long course of his work on transects, the data that had been computerized was transferred more than once from one program to another, resulting in data sets in a variety of formats and often with extraneous information needing removal. At the Garden, Oliver Phillips undertook the difficult task of reorganizing previously computerized data and insuring that information from the other sites was entered into the same format. All of the data was either entered or converted to consistent computerized format by Nancy Hediger.

The Garden will make all of the transect data available via the World Wide Web (http://www.mobot. org), so that researchers can either access information from individual sites or download regional sets or the entire collection. Oliver Phillips and I are preparing a book to present the results of the data analysis, with an introduction covering the historical background and the rationale and methodology of the transect data. The bulk of the book will consist of single-page data summaries for each transect site, and the volume will be published in the *Monographs in Systematic Botany from the Missouri Botanical Garden* and entitled *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set.* It will serve as a companion volume to the computerized set of transect data available on the World Wide Web.

The list of Gentry's publications that follows is as complete as possible. However, at the time of his death, he was actively involved in a large number of collaborative projects, and many of his collaborators continue to include him as a coauthor. He also had contributed treatments of various taxa to a variety of floristic projects that have yet to be published. Thus, his list of publications will continue to grow beyond the number included below, and will include contributions in the Gentry Invitation Series. To document the extent of Gentry's involvement in the training of botanists, a list of all his students and their projects, compiled by W. G. D'Arcy, follows the publications list.

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Bignoniaceae. *In* Gardens of Hawaii.

Flora of Capeira and the Guayaquil Region. Banco Nacional, Quito. [With C. Dodson.]

Roundtable on Tropical Forests. Bioscience. [With C. Peters & R. Mendelsohn.]

Bignoniaceae. *In*: Flora de Nicaragua.

Apocynaceae. *In*: Flora de Nicaragua.
Humiriaceae. *In*: Flora de Nicaragua.
Passifloraceae. *In*: Flora de Nicaragua.
Bignoniaceae. *In*: Flora de San Juan.
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Bignoniaceae. *In*: Flora de Colombia.
Amazonian plant diversity and endemism: The conservational significance of B-diversity and explosive speciation. *In*: G. Prance (editor), Proc. Manaus Workshop on Amazonian Conservation.
Biodiversity of Peruvian Amazonia: Problems and opportunities. *In*: K. Mejia (editor), IIAP Symposium Volume, Iquitos.
Species richness and floristic composition of Chocó region plant communities: An update. *In*: P. Leyva (editor), Colombia: Una mirada al Pacífico.
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Figure 2. Gentry in his office at the Missouri Botanical Garden in 1993.

Graduate Students Supervised by Gentry (with Thesis Title)

Henry Rodriguez, M.S., Washington University, 1977 [degree not completed].

Michael Zimmerman, Analysis of the Reproductive Strategy of *Polemonium* in Colorado. Ph.D., Washington University, 1979.

David Lorence, A Systematic and Eco-evolutionary Study of the Monimiaceae in the Malagasy Region. Ph.D., Washington University, 1980.

Franklin Ayala, No thesis. M.S., Washington University, 1982.

Valerie Kapos, An Ecological Investigation of Sclerophylly in Two Tropical Forests. Ph.D., Washington University, 1982.

César Barbosa, Revisión Taxonómico de la Sección *Caulanthera* (*Zygia* Browne) del Género *Pithecellobium* Martius (Leguminosae–Mimosoideae) en Colombia. M.S., Universidad Nacional de Colombia, 1984. (Co-directed with Enrique Forero.)

Clement Hamilton, An Ecosystematic Study and Revision of *Psychotria* Subgenus *Psychotria* (Rubiaceae) in Mexico and Central America. Ph.D., Washington University, 1985.

Donald Faber-Langendoen, Combining Conservation and Forestry in a Colombian Rain Forest: An Ecological Assessment. Ph.D., Saint Louis University, 1989.

Ricardo Rueda, Revision of the Genus *Clerodendron* (Verbenaceae) in Mesoamerica. M.S., University of Missouri-St. Louis, 1989. Systematics and Evolution of the Genus *Petrea*, Ph.D., University of Missouri-St. Louis, 1993.

Washington Galiano, The Flora of Yanacocha, a Tropical High-Andean Forest in Southern Peru. M.S., University of Missouri-St. Louis, 1990.

Gracielza Dos Santos, Systematic Wood Anatomy of Tecomeae (Bignoniaceae). M.S., University of Missouri-St. Louis, 1990.

Richard Clinebell, The Biology of Exotic Invasion into the Wade Tract, a Relict Longleaf Pine Savanna. M.S., University of Missouri-St. Louis, 1991.

Oliver Phillips, Comparative Valuation of Tropical Forests, Ph.D., Washington University, 1993.

Current students (at time of death):

Brad Boyle, Washington University. Studying now under P. Mick Richardson

Laura Marsh, Washington University (co-directed with R. Sussman)

Carlos Reynel, University of Missouri-St. Louis. Received his Ph.D. under P. Mick Richardson, Systematics of Neotropical *Zanthoxylum* (Rutaceae) with an Account on the Wood Anatomy of the Genus, Ph.D., University of Missouri-St. Louis, January 1996.

Jennifer Hedin, Washington University. Studying now under P. Mick Richardson

Ivón Ramírez, University of Missouri-St. Louis. Received her Ph.D. under P. Mick Richardson, Systematics, Phylogeny, and Chromosome Number Evolution in *Cryptanthus* (Bromeliaceae), June 1996.

Jason Bradford, Washington University. Studying now under Paul Berry.

—James S. Miller, Missouri Botanical Garden, St. Louis, Missouri.

Figure 3. Gentry and friend in Madagascar.

The Memorial Service

It was my pleasure to be Al Gentry's first teacher in the world of botany. Al was born and grew up in Clay Center, Kansas, a small town in the north-central part of the state. He graduated from the Clay Center high school in 1963, and as is common in that part of the world, he came that fall to Kansas State University in Manhattan, Kansas. He arrived with superb recommendations, for he had been regarded as a brilliant student in high school. Al was not sure what he should study in college, but being a capable boy in a small town carried certain assumptions, and one was that he should major in physics. Al took courses in physics and did very well; he also did well in chemistry and molecular biology, where for a while he had an undergrad student job in a laboratory. He was interested in anthropology, but he earned a "B" in an anthropology course and so concluded that anthropology was not his field.

Al was associated with the then-popular "honors program," and there is where I made his acquaintance. He was a part of an honors seminar group that was centered on tropical biology, the role of the tropics, and related matters. In the course of the term, he and I began to talk about plants, he began to hang out in the Herbarium, and he became fascinated with what plant taxonomists do.

Students who were juniors in the honors program were encouraged to take on an "honors project," and especially a project that related to some ongoing research program in the University. Al looked into the Herbarium for a possible honors project, and particularly for one that might involve his background in the physical sciences. At that time, Kansas State had a program to study radiation and radiation shielding that were a part of nuclear power plants, and there was a radiation shielding laboratory in the rolling hills just a few miles west of town. The people who directed the research at the site were interested in learning if the radiation from the site affected the nearby biota, so Al formulated a project wherein he collected plants, identified them, mapped their distributions on the site, and compared his data to those from undisturbed or non-radiated tall grass prairie. The results were presented as his honors seminar, but as he was wrapping up his work, he wondered if the radiation caused the observable differences in plant distributions, or if the differences were attributable to disturbances from the construction of the site. He could not solve that particular question, but he had done some research on his own that involved a definable problem, a clear set of procedures, the techniques to carry them out, and some support from the Department of Nuclear Engineering. It all fit together nicely, and it led Al into a career in systematic botany.

Al graduated from Kansas State University in June 1967, with two degrees, a Bachelor of Arts and a Bachelor of Science, both *magna cum laude*. He was capable, articulate, ready to talk about anything, perhaps a bit ornery, and obviously going places in systematic botany. We at Kansas State assisted in sending him to the graduate program at the University of Wisconsin, to work with Professor Hugh Iltis, and, as may be said, "The rest is history."

Some years ago, a fellow who had just returned from a stint in the tropics came to the Herbarium at Kansas State, and he brought with him a sack of mangoes. We sat at the lunch table and chopped up the mangoes and ate them. Somebody said, "Hey, taste this one—it REALLY is good," and sure enough, that one mango was truly excellent. One of the Old-Heads there said, "There is a funny thing about mangoes, for once you find a really good one, you will remember it forever, and you will spend years searching and waiting for another one that is as good." Al Gentry was our Good Mango. We look forward and wait for another good mango, or for another Al Gentry.—*Theodore M. Barkley, Kansas State University*

On November 21, 1966, I got a letter from one Al Gentry, a senior at Kansas State University in Manhattan, who informed me that his botany professor, Theodore Barkley, suggested that he might like to do graduate work with me in Wisconsin, that he had a G.P.A. of 3.9 and . . . "do we have a fellowship" for him? I wrote him right away and said that would Mr. Barkley write me a letter outlining all his sins and virtues, and for him to tell me what he was interested in: the tropics? Wisconsin floristics? a summer in Costa Rica? whatever? Three days came the reply, in Gentry's very small handwriting: "I have enclosed a copy of the personal essay that I wrote for the Woodrow Wilson Fellowship, I think it will cover all of your questions, even though Dr. Barkley about flipped the number of 'I(s)' in this essay, there are lots of 'I(s)' in there."

Indeed, Alwyn Gentry did not hide his capabilities, then or later. Nevertheless, this was a very interesting essay, six pages long and exceptionally well written. To him, first of all, the beauty of nature and the stimulation of science were his chief intellectual concerns: "I need to be out of doors as much as possible, just to be close to the sheer beauty of

the natural world . . . to feel the mysterious perfection of the organisms, the how and the why." "Botany, intellectually, is pleasing to me because of its great emphasis on evolution and ever since I have been a preschooler I have been a taxonomist at heart."

His second consideration, he writes, "is my desire for physical adventure with tropical plants, tropical field trips, the chance to be away from civilization exploring little-known jungles and discovering exotic new species."

But then, also, in a total switch, "I feel a very strong desire to be something more than just a scientist. . . . I want to be able to justify the importance of my work to myself and others, and as a college teacher I want to stimulate others to question why they are students and consider their debt to society."

Now, I am a bit of a moralist myself and, as an old environmentalist, I have fought many an environmental battle. But now here comes this young man from the flatlands of Kansas, this boy, barely 21 years old, writing a professor in the flatlands of Wisconsin, not only about physical adventures in little-known jungles away from civilization (that alone would pique my interest), but also professing there, for one so young, quite astonishing sentiments.

And yet, at the very end he returned to his main theme: "The collecting and field study of tropical plants also presents the challenge of physical adventure in tropical jungles. . . . The mystery and excitement of unknown places excites me very much, beyond anything else. [And now, get this!] After receiving my doctorate degree, I hope to reevaluate the whole taxonomic system now in use so as to give it a better portrayal of true evolutionary relationships."

When I read this, I said to myself, "My God," I mean, who does he think he is? What have you done, Ted Barkley, to this innocent kid? I showed Gentry's letter and fellowship application to Paul Allen, our Chairman, who scribbled on the top of it the understatement of the year: "This chap has possibilities!"

Well, I finally did meet up with this Wunderkind, when, arranged by Barkley, I gave a speech at Kansas State on April 6, 1967 (Iltis, H. H. 1969. A requiem for the prairie. *Prairie Naturalist* 1(4): 51–57), with Gentry in the audience. In that rather inflammatory talk, I urged the students in Manhattan to become environmental activists, to fight for a series of 1-million-acre Prairie National Parks, to stage "UC Berkeley" protests on agricultural campuses to force intellectual change, to revolt against the environmental ignorance of their stodgy teachers. The chancellor sat through the whole thing, and looked like had been eating sour apples. Afterwards, Al was introduced to me, a thin young man, pale, hungry-looking, intense, and, I felt, somewhat uptight, and very, very ambitious. He liked the speech. And so it came about that Al Gentry chose the University of Wisconsin to become my graduate student. And when he first visited Madison for a week in June of 1967, we arranged for him to take the OTS in Costa Rica, which, for one who wasn't even a student yet at the UW, was very unusual. But somehow we finagled travel money for him to get to the tropics, finally, and the rest is history.

I need to add here something about his letters of recommendation. According to Prof. Lloyd Hulbert, Al was "exceptionally intelligent, among the most gifted students" he has ever had but ". . . careless in the minor details in his work, because in fact this is the result of the feeling that such things are unimportant for him to bother [with] in the big

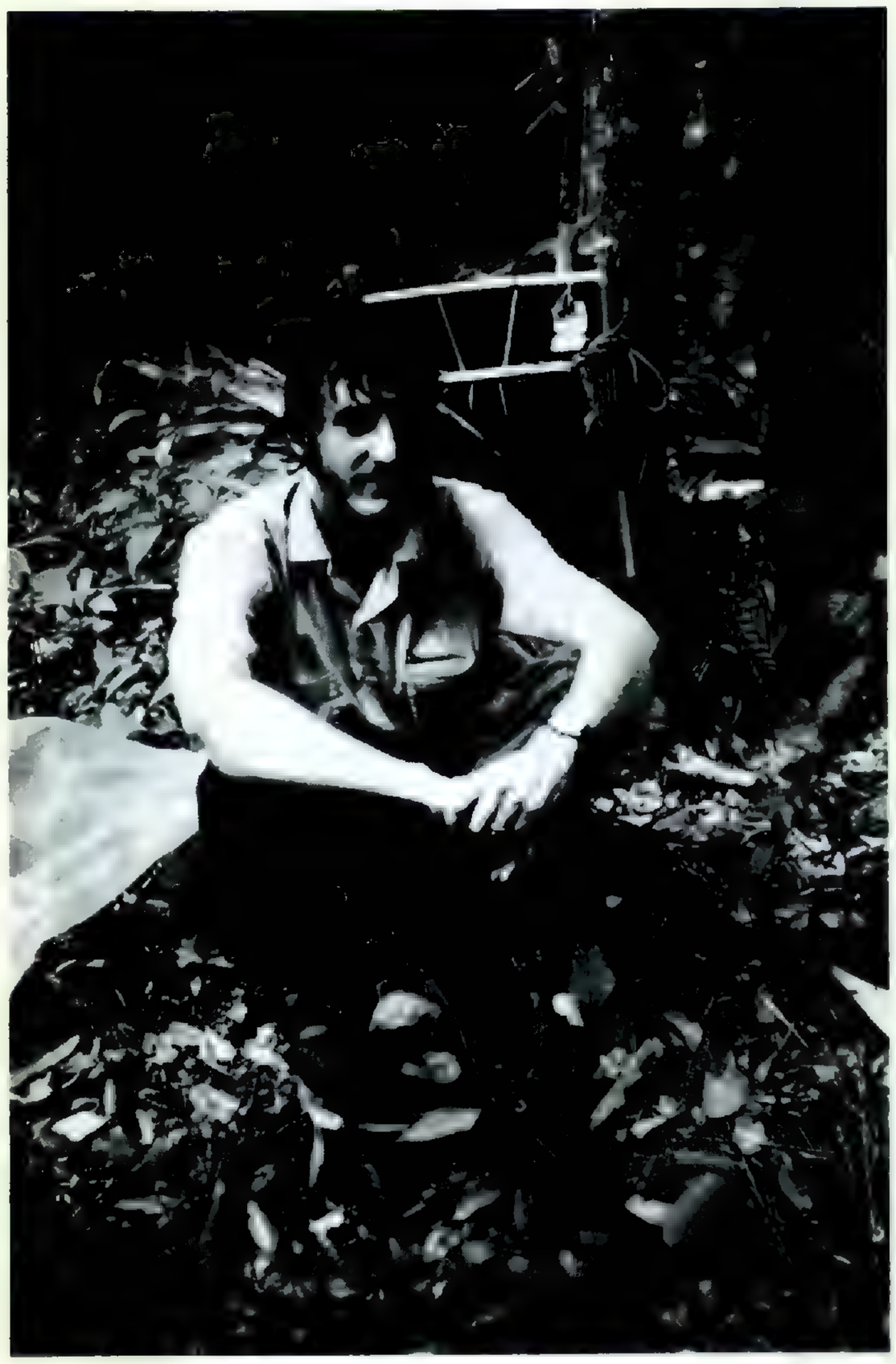

Figure 4. Gentry on Cerro Tacarcuna along the Panama/Colombia border. Gentry conducted the first botanical exploration of the mountain in 1975 and discovered many new species.

scheme of things." And this is of course the paradoxical glory, in a way, of much of Al Gentry's work. That he saw the big picture and became this fine taxonomist and global ecologist. Ted Barkley, his major advisor, wrote that, "If there is one word to criticize him it would be that he is perhaps over confident or even somewhat conceited. However, this may be only a natural product of being a brilliant and competent young man."

Well, I had other problems in that fall of 1967, I got divorced, that's always difficult, there was always something going on; in short, I didn't pay much attention to Al. But he got all A's the first semester, and he got all A's again the next semester.

While visiting us that June, Al was looking for a research project. I wrote my friend, Russ Seibert, a graduate of the Missouri Botanical Garden, and then Director of Longwood Gardens in Pennsylvania, who once upon a time studied Bignoniaceae, and asked him if he or anybody else was now working with this family. And when he said "no," I suggested to Al that he might have a look at it once he got to Costa Rica.

Well, as many of you know, Al fell in love with the Bignoniaceae. He started to work on a revision of Central American *Tabebuia* in the spring semester of 1968, worked very fast and furious, and soon told me in no uncertain terms that he's going to be done with his master's thesis by the end of the summer. That declaration caused our first big blowup. I told him that, "At UW, it takes two years, so there is no way you can do it in one." "Oh yes, I can." "Oh no, you can't." I mean, I said, "I am the professor here and you are the student [genius or not], and it takes time to write a good thesis." But anybody who ever knew Al Gentry may appreciate that confrontation; he was enormously stubborn, absolutely confident that whatever he wanted to do he was going to do it. Well, I have similar attributes, and I was older, which had its advantages. So, instead, that summer we shipped him off to Miami, Florida, to take a tropical botany course. In the fall of 1968, he was really going at his *Tabebuia*, finished his thesis in record time, and by Christmas, finally got his master's degree in plant taxonomy. But Al, from early on, was also an ecologist, and the very first paper he ever published, for OTS and while still at Wisconsin, was a comparison of leaf shapes between dry and wet forests in Costa Rica.

But ominous events were about to overtake him. The war in Vietnam was in full swing, people were getting drafted, including Al. We talked a lot about this because he did not believe in the war, did not really feel that he would like to collect plants in Vietnam, at least not under those circumstances!

In the meantime, that fall, he brought a lovely young lady to Madison, his childhood sweetheart, Julie. Professor Lenn Thien and his wife and I threw an engagement party for them, a very interesting affair as it turned out, because they were both so shy. I bought some bottles of champagne to loosen things up a little. I think Al came from a "dry county" in Kansas that didn't permit alcohol, and my strategy didn't work: they hardly touched the stuff, and both just sat there, totally serious, shyly looking at each other, for three whole long hours, no matter how many jokes I cracked.

So, that Christmas, right after Al graduated with his master's degree, the couple got married, took a quick honeymoon trip to Costa Rica and Panama to collect more plants, and then off into the Army. By April 7, 1969, he was in Fort Leonard Wood, Missouri, a little bit later in Fort Sill, Oklahoma, where his wife by then had joined him. Eventually he ended up at Officer's School in Fort Belvoir near Washington, and, on completion, was offered a commission as a second lieutenant. But this promotion he turned down, for several reasons; in any case, he did not want to go to Vietnam. By then, we were all writing letters to the military that Al had to support his widowed mother, and also that he was needed to teach botany in Madison. And so, not any too soon, we got him out of the Army and back into botany.

It was now the summer of 1970, and Al was undecided whether to return to the UW or not. It all depended on getting a fellowship. To make a long story short, he was bribed (I hate to put it this way) by Walter Lewis of the MBG to come to Missouri, with money we could barely equal. After many letters, back and forth, about the needed support, Walter then offered him not only a fellowship but also travel funds, apparently "unlimited travel funds" is what he promised. That did it! I didn't believe it, but what else could I do except wish Al well? In retrospect, it was a good decision. It was time for us to part.

Let me wrap up this sad duty with a note that I wrote to the library here, and to Peter Raven: I am giving a set of all my 25 years of correspondence with Al Gentry to the MBG library, sending it to the place where he not only earned his Ph.D. dealing with his beloved trumpet vine family, but also where he was able to really spread his wings and learn to fly like a botanical Jonathan Livingston Seagull; that is, do impossibly productive feats in all too short a life. Fate was very kind to this brilliant, complex and contradictory man, who not only escaped by hair's breadth being sent to Vietnam and possibly death, but who, were it not for the

tolerance, or wisdom, of the Missouri Botanical Garden might well have suffered the fate of many another maverick biological genus and disappeared somewhere into relative obscurity. But the lives of Gentry, perhaps the greatest tropical ecotaxonomist, and Peter Raven, arguably the greatest botanical organizer, intersected in their planetary orbits just at exactly the right time, in 1972 or so, shortly after Raven became Director of the Garden and Gentry needed a permanent position, a platform from whence to take off.

And now, all too soon, we mourn Al Gentry's untimely death and our great loss. What could he not have accomplished in the next 20 years! There will not be another one like him in our lifetime, and we are all grateful for what he has given to the world. And we must also say thanks, finally, to Peter Raven and to the Missouri Botanical Garden for putting up with and supporting, this driven and difficult small-town Kansas boy, who from grade school on yearned for excitement and dreamed of adventure, and found more, finally, than he could have ever hoped for.—*Hugh H. Iltis, University of Wisconsin*

Al Gentry's interest in the Bignoniaceae was kindled while at the University of Wisconsin. It was during this time, in the fall of 1968, when he was completing parts of his thesis at the Smithsonian Institution, that I first met this enthusiastic and energetic student of plant biology. Thanks to Hugh Iltis's many stories of St. Louis, some great and some not so great but undoubtedly absolutely true, we were fortunate enough to bring Al here in 1969 at typical warp drive even then. I feel certain that Al would have revised the whole 112 genera of Bignoniaceae if some brakes had not been put on his Ph.D. research scope. Even so, using detailed ecological studies of mostly new data on edaphic limits of distribution, floral phenology, floral morphology, pollinators, and fruiting strategies, his systematic treatment included a detailed analysis of no fewer than 85 Central American species. A study of the family and a number of little-used taxonomic characters, apparent only from field observations, were also incorporated into his dissertation in arriving at systematic and phylogenetic conclusions.

The dissertation was 769 pages long, plus 184 full-paged figures: without hard covers it weighed 9-3/4 pounds and was 4-1/2 inches thick. Lest you think we only weigh and measure dissertations when awarding degrees at Washington University, be assured that at least in Al's case his research did indeed involve extraordinary scholarship, both in quality as well as mass. I perhaps dwell too long on Al the Ph.D. student, but I think that what he accomplished then epitomized what he was to do in the future: his great interest in plants as interactive parts of complex ecosystems, his acute observational powers rarely if ever lost from his memory bank, and last, but not least, his ability to impart this knowledge with clarity of thought. Such aspects were clear to me and other members of his committee when Al graduated in December of 1972 to take up his position as a curator at the Missouri Botanical Garden.

I must add one anecdote about Al's dissertation known to very few, except Julie and perhaps their children, and one which graduate students in particular might appreciate, for pitfalls befell even Al Gentry when he was a student. Quoting from his letter to me of June 30, 1972, he said, "I feel there must be a cloud of bad luck hovering over me: the [original] copy of the thesis I had with me was stolen along with a suitcase full of clothes in Copenhagen [Al was visiting European herbaria examining types of Bignoniaceae]. Now with the fire at Summit, I may really be wiped out [referring to the Garden's herbarium and living quarters in the old Panama Canal Zone where Al was acting curator while doing his fieldwork, which burned while Al was in Europe]. I'll let you know as soon as we get back to Summit whether you've still got a terminal grad student or one who is more or less starting over again. . . . Believe me we've got our fingers crossed." Well, it turned out that Al did not have to redo his research, for the only carbon copy survived the fire in a file cabinet with only limited water and smoke damage, but it had to be retyped by Julie; remember, this was the age before computers.

Over the years Al's interest in teaching and directing graduate students' research expanded with his career. He was deeply committed to our academic program in biology at Washington University as well as later at the University of Missouri-St. Louis. Whenever possible he participated in our faculty meetings as an Adjunct Professor in Biology, but his greater contribution came with his dedication to graduate students seriously interested in plant systematics and ecology. Al taught them well individually and through his two courses, "Phytogeography" and "Structure & Composition of Tropical Forests," and a seminar in Floristic Taxonomy, one I developed many years ago, which Al continued to give from the 1970s on. When not in the field, he was available for in-depth discussions and reviews of classwork and research, and he gave his time freely for determining specimens to genus and

Figure 5. Gentry with José Schunke in Tocache Nuevo, Peru, in 1979.

species, even very incomplete ones, with amazing skill and speed. This does not suggest that Al enjoyed being pestered, especially by those who did not learn after the first or second attempt, for Al did not "suffer fools gladly."

An aspect of our association, which will not be found in our professional curriculum vitaes, is that we belonged to the same undergraduate fraternity, Alpha Tau Omega. I mention this for two reasons: first, because Al received at least one coveted award from the fraternity as an academically top senior at Kansas State, a fact which comes to no surprise to anyone here, and second, because it provided a very special link in our relationship which meant a great deal to both of us.

For his family, for his associates at Washington University, the Missouri Botanical Garden, and elsewhere, and for me, Al's death is very much a compounded loss, because we have lost not only a friend, we have also lost a truly exceptional colleague, who devoted his life to the making of a brighter and greener planet for humanity.—*Walter H. Lewis, Washington University*

Al Gentry's death shocked the scientific community. This is shown in a message I received from Dr. Ariane Luna Peixoto of the Universidade Federal Rural do Rio de Janeiro, Brazil, one of Al's closest friends in Latin America. She says: "For Brazilian botanists, particularly those working on the Atlantic coastal forests, the passing of Al Gentry constitutes a source of undescribable sorrow. Gentry was our friend and our teacher. A devoted teacher who would teach us from far away through his very detailed letters as well as through his publications, and from close by in our classrooms and tropical forests. Speaking in a mixture of English, Spanish, and Portuguese, in field trips and in the classroom, he never neglected anything. He was always willing to share his knowledge. For us Latin Americans, he took the mystery out of many things. He showed us that plant identification in the field can be simple and easy as long as you have the commitment, as long as you develop the capacity to observe and, above all, as long as you love what you are doing. He showed us that phytosociological sampling in tropical forests can be carried out in a

quick, efficient, and correct way, as long as you are willing to go beyond your own physical abilities. He showed us that inventories and phytosociology are also taxonomic tasks that can be used to great advantage in monographic research. Al Gentry was a role model. With his departure, we have a difficult but important task before us: to try our best to reach his level in our own professional lives."

I knew Al during his entire professional career. We both received our Ph.D.s in 1972. It was in late 1972, during the Annual Systematics Symposium, that I met him here in St. Louis. At that time, and at Peter Raven's suggestion, Al and I agreed to develop a joint research project in the Chocó region of Colombia. It would be a cooperative effort between the Missouri Botanical Garden and the Institute of Natural Sciences of the National University in Bogotá, where I worked.

It didn't take long for Al to show up in Colombia. Early in January of 1973 I received a phone call from St. Louis. It was Al, telling me that he would be in Bogotá in a couple of days (actually, on January 5th. I was on vacation!), and that he would like to be in the field in Chocó, with me, by the 6th! Somehow I managed to get plane tickets for both of us for the 6th. He arrived on the 5th, spent the night in my apartment, and we flew to Quibdó the following day. We spent the next five days collecting in central Chocó. This was the beginning of what we considered at the time one of the most successful joint programs in botanical research between a North American institution and an institution in a developing country. Al and I were together in the field in Colombia perhaps as many as five times. But the program lasted for twelve years. During this time we provided training for several Colombian and U.S. students, helped establish a herbarium in the city of Quibdó, initiated some small-scale field research by local botanists, collected over 17,000 numbers (more than 80,000 herbarium specimens) between the two of us, and brought the attention of the scientific community to this poorly known but extremely rich region in terms of biodiversity.

Al's eagerness to be in the field is well known. He was not particularly interested in public relations, meeting people, or spending time in big cities. He wanted to be in the field. In fact, for at least the first two years of his involvement in Colombia he seldom spent more than a day in Bogotá. As a result, no one at the Colombian National Herbarium knew him. I had a hard time explaining to my colleagues that Al Gentry really existed! Finally, I decided to "kidnap" him for a few days so that he could meet the local botanists.

He was extremely strong in the field. I remember a time when Al, Andrew Sugden (a British student), Douglas Daly, and myself were in Chocó, exploring the foothills of the little known Cerro Torrá. Basically without food we traveled for hours, until most of us were exhausted. Andrew, Doug, and I actually decided to give up our collecting. We sat down to rest and to try to recover our strength. Al kept on going, and several hours later came back having found a place for us to spend the night. We then were up until 2 a.m. pressing plants. Pressing plants at night was something he seemed to enjoy. Even with our poor performance in the field that day, we had managed to collect nearly two hundred numbers!

To be sure, Al and I had many differences of opinion. A couple of examples of a fairly mild nature will serve to illustrate this point.

One of the many positive results of our work in Chocó was the publication of the "Chocó Checklist" (Forero & Gentry, 1989). However, bringing this checklist to completion was not an easy task because, as we all know, Al was stubborn when it came to taxonomic matters. He would not accept, for example, the subdivision of the genus *Cassia* into three genera as proposed by Irwin and Barneby (1982). As someone interested in the family Leguminosae, I was happy with their classification. Al wasn't. In the end I was forced to give up and include all the pertinent species under *Cassia* in order to see the checklist published. Not two days had passed since the checklist was published when I received a letter from Rupert Barneby asking me if we were out of touch with taxonomic literature!

Al and I used to argue because he blamed me for rating my students too high. Who did not hear him say that *his* students were all wonderful, *the best*!? The truth is that we both had excellent students.

Our lives followed somewhat different but parallel paths. My life has been more devoted to the administration of science. His was devoted to his research. I am glad that I was able to contribute to his scientific accomplishments as we worked together in Colombia. I am also grateful for the opportunities I had, as an administrator both in Colombia and at the Missouri Botanical Garden, to help him in some way to continue to fulfill his scientific dream. But more than that, I am glad that I can remember him as a wonderful colleague and as a friend.

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Figure 6. Gentry with Rudolfo Hindo and Charles Myers, head of the department of herpetology at the American Museum of Natural History, unloading equipment at Yaviza, Panama, on one of Gentry's expeditions into the little known Darién.

Irwin, H. S. & R. Barneby. 1982. The American Cassiinae. A synoptical revision of Leguminosae Tribe Cassieae subtribe Cassiinae in the New World. Mem. New York Bot. Gard. 35, parts 1–2: 1–918.

—Enrique Forero, Universidad Nacional, Bogotá, Colombia

When I gave my first presentation at the Missouri Botanical Garden in 1983, I showed some slides of medicine men and said that these people can identify every species in the forest without looking at the fruit or the flowers and that no university-trained botanist could ever hope to do that. Almost before I was even finished this skinny guy had come racing down to the podium, shook my hand, said I'm Al Gentry and I can do that. So I handed him a pile of these miserable sterile specimens that the Indians had given me: a piece of bark here, a piece of leaf there, and within minutes Al had identified everything to species.

I gave a talk at the American Horticultural Society two days after the accident. I started out by asking how many people knew that a basketball player died a month ago of a heart attack, and almost every hand in the audience went up. I then asked how many people knew that the greatest tropical biologist who ever lived died in a plane accident two days ago, and about 20 hands went up. I truly believe that says something terrible about our culture and who our heroes really are. We worship sports figures and politicians, and we have guys like Al Gentry and Ted Parker who don't care about money, don't care about clothes—they just want to make the world a better place. When people die in the military it is said that they gave their lives for their country, but what did Al and Ted give their life for? They gave their lives for everybody and for the planet. They were always pushing the edge of the envelope and they paid for it with their lives. Al and Ted were heroes in an age without heroes.

The most incredible display of biological expertise I have ever seen was in a meeting at the World Wildlife Fund about eight years ago. WWF had invited 30 top scientists to discuss Andean priorities. Despite all the charismatic megavertebrates around the table, Al and Ted started out in northern Venezuela and walked down the Andes peak by peak, valley by valley. This is top priority, the narcos are here forget it. Nobody's ever been here, we have got to go there. They made the rest of these guys superfluous. In fact, it was humiliating to be a sci-

entist in the room with Ted and Al that day because if they had taken those other 28 guys and pushed them outside, it wouldn't have made any difference. When they died, Russ Mittermeier said 75% of the unpublished information that exists on the biodiversity of Andean forests was lost with Ted and Al.

Jim Duke just finished a book on Amazonian ethnobotany with a dedication to Al that I'd like to read: "Our book has been enhanced by the taxonomic foundation provided by the arduous and intensive perseverance of the late Dr. Gentry. He would not rest until he named an unknown forest giant. . . .We respectfully but sadly dedicate this small volume to a fallen forest giant, Al Gentry, friend of the forest and teacher to many of us, trying to save the forest that survives him. The Amazonian Center for Environmental Education and Research (ACEER) will dedicate their 250,000-acre forest reserve to his memory. The forest that kept him going like a robot swallowed him up. But his spirit lives on, and will help in the difficult efforts to save the forest of today for the children of tomorrow. Few of us can view any attractive bignoniaceous vine without recalling the ethereal spirit of Al Gentry and the forests he represented. Long live the forest and spirit of Al Gentry" (Duke & Vasquez, 1994).

When I spoke at Ted Parker's funeral service last weekend, I read a line from Tennyson: "Those whom the gods love die young."

I don't know if the gods loved Al and Ted, but I sure did.

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—Mark Plotkin, Conservation International

I graduated from Washington University and Alwyn Gentry was my doctoral advisor for five years. Scientists like Al are very rare—he has tackled so much, taking everything to the limit and then beyond, exploring new fields and new horizons, and through his field guide unlocking the mysteries of the neotropical forests for us all. A scientist that special who is a great teacher as well, who has devoted so much time and energy and enthusiasm to their students around the world, is truly unique. People like Al and Ted are rarer than gold, and we know what a terrible loss this is.

It would be hard to overstate Al's influence on botany students in the Americas. In 21 years as a curator, he had at least 20 doctorate and master's students at all three of the universities affiliated with the Garden—-Washington University, University of Missouri-St. Louis, and St. Louis University. Although as a researcher Al had been going full steam ever since his undergraduate days, as a teacher his responsibilities were snowballing. When he died he was supervising theses by no less than nine students, and had recently taught graduate courses in St. Louis and Latin America (Peru and Colombia).

Several qualities come to mind when I think of Al Gentry the teacher, qualities that made him truly special. There was his tremendous enthusiasm, excitement, and knowledge about plants and forests that drew like-minded people to him. Al went all over the world, botanizing like a man possessed, and took students in each country into the field with him. Here was someone who could convince even the most confirmed urbanite of the essential wonder of the natural world. During these field trips it was impossible not to be inspired by his excitement, and so from all over the world students came to St. Louis to learn from Al Gentry and his colleagues here! Other students came to meet the man whose botanical zeal they had only heard about through some of the Gentry legends. Ted Parker used to tell the story of how Al once fixed his sights on collecting an unusual looking epiphytic bromeliad, 20 meters up a tree. Climbing up, he put his hand in it from below, and felt a sharp pain. Cursing the spiny plant that he thought had pricked him, he put his hand in again only to get it cut again. After this happened a few times, eventually he realized that rather than being cut by the plants' leaves, he was being repeatedly bitten by a venomous fer-de-lance! He survived that encounter of course, to the great benefit of his students.

Al cared deeply about his students, not just academically, but also about our welfare. For students coming from abroad, the culture shock arriving in the United States can be pretty severe. But he was always there if you wanted him for personal advice. Since his office was always open, people would troop in, in a fairly uninterrupted stream, and he managed to find time for all of them. One of the strongest memories I have of Al is of him wryly smiling, as he sits at his desk which is piled two, three, maybe even four feet deep with specimens, and manuscripts, and papers, and enormous amounts of work, and a small queue of students and curators in his office wanting to bend his ear. There he was with dozens of projects on the go at the same time, and he was still willing to talk with you about what you wanted to talk about.

The description of Al as a fallen giant forest tree is so right, perhaps it is something we have all

Figure 7. Al Gentry teaching a group of students at Von Humboldt in Peru.

thought about. He was always searching for new light, for new growth, and new inspiration. He was a forest giant and most of us who studied under him and who worked with him, really were privileged to be around this forest giant. When he died it crashed down and left a huge gap in the forest, an enormous gap. When we first learnt of his passing, we thought that we could never fill this huge hole, it is too big. But the more we think about Al and what he has done to teach others, of the many students not only here but all over the world, thousands and thousands of people he has inspired to dedicate their work to the tropical forests, we hope that perhaps we can fill that gap eventually. But we had better do it quickly for the sake of giants like Al who cared so passionately.—*Oliver Phillips, University of Leeds*

I was a graduate student with Al Gentry for six years, and I graduated two days before he left for his last trip. He taught field and classroom courses at many universities throughout all of Latin America. On the field courses and collecting trips, he was a tireless plant collector and a minute-to-minute teacher. He was not always a serious person. Once in a while he would tell you a quick joke and then return to talking about plants. The teaching would include anything related to plants, such as nomenclatural problems, phytogeography (one of his favorite topics), ecology, and so on and so forth. He realized that one way to do conservation of biotropical diversity was teaching and learning from others. Whenever you talk to people who have met Al, they will tell you how good he was as a botanist and as a teacher, and this was because Al believed in just teaching and passing on his experience gained from years of travel and research in Latin America.

In the field, he was always accompanied by students and botanists from local institutions and he would always talk to them about ideas and projects. He encouraged many people to do research in the tropics, and in some cases he suggested topics to the students. He also encouraged many of us in the tropics to study abroad. He helped students get enrolled at foreign universities, and in many cases he was also our thesis advisor. As a major professor, he was one of the best, helping students despite the fact that he was always very busy. For example, to come to his office to talk about the thesis or about any scientific problem no student needed an appointment. When he knew the dates he would be out of town, he would come to his students and tell them, so that they could come to his office to clear up urgent situations. In some cases, when he went

away for two or three months and the students were working on their theses, he would say, "Write all your questions down and we will talk about them when I come back." If the students had a document ready to be revised by the advisor, Al would take it and put it in his briefcase and read it at the airports while waiting for a flight, and then would send it back by mail a couple of days later. That was Al! If the students for some reason did not come to see him after he returned from a trip, he would come to the students' cubicles to see how the thesis work was going. He was also very warm—he would ask you about your thesis and about your personal problems that he could help to solve.

Another way Al would help his students was letting them use his grant money to travel for their own research activities and for publications. Many of us as students made our first formal publication because Al encouraged us to do it. He would say, "It's so easy, and after the first one you will be a professional. For example, to publish a paper on a new species is a piece of cake. Just take the Botanical Latin book and write the Latin description and then write a complete description in English, bring it to me and I will give it a quick look, and that is it." It took me a while to believe this, but one day he came to me and said, "Hey Ricardo, I got an *Aegiphila* from Colombia, I believe it is a new species. Please check it. You know, if it is a new species this is your opportunity for your first paper. There is only one problem, if it is new, I need a name soon since it is a collection from my plot project in Colombia." Taking into account his great experience, I checked everything about the collection, but I knew from the beginning that it would be new. I wrote the paper and he helped me through the process. When it came out in *Novon* he came to me and said, "Did you see the paper?" I said, "Yes, I am so happy." And he said, "Now you can go on without problems."

Another Al tradition was to celebrate the theses defenses of his students. Everybody in the Garden knew about the famous pizza party after the student's defense. I remember my party, two days before he left on his last trip, and I remember Al talking very highly about his students. He was very proud of them, and we were also proud of having as our advisor the best modern tropical botanist, the man that had a continental view of the flora. Unfortunately, we have lost Al and we are all sad, but we also know that if he were in this room, he would say it is not the time to be sad, it is time to work. We say to you, Al, that you are alive in every one of us. You trained many people in Latin America and we will keep your scientific legacy alive with us forever.—*Ricardo Rueda, Universidad Nacional Autónoma de Nicaragua-Leon*

Eulogy

In thinking about Al Gentry at 22 years old, going to the tropics for the first time after longing to do that for several years, and with so much love for biology, 22 years old on his way between the plains of eastern Kansas and the forest, perhaps, of Madison, I was thinking about how he must have felt, and I was reminded of Darwin. I looked up what Darwin said on February 29, 1832, when he was on the voyage of the Beagle and he got to Bahia in Brazil, and Darwin said,

> "The day has passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has been wandering by himself in a Brazilian forest. Among the multitude of striking objects, the general luxuriance of the vegetation bears away the victory. The elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliage, all tend to this end. A most paradoxical mixture of sound and silence pervades the shady parts of the wood. The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore; yet within the recesses of the forest a universal silence appears to reign. To a person fond of natural history, such a day as this, brings with it a deeper pleasure than he can ever hope again to experience. After wandering about for some hours, I returned to the landing-place; but, before reaching it, I was overtaken by a tropical storm. I tried to find shelter under a tree which was so thick, that it would never have been penetrated by common English rain; but here, in a couple of minutes, a little torrent flowed down the trunk. It is to this violence of the rain that we must attribute the verdure at the bottom of the thickest woods: if the showers were like those of a colder clime, the greater part would be absorbed or evaporated before it reached the ground. I will not at present [and this is a sentence I think is particularly appropriate] I will not at present attempt to describe the gaudy scenery of this noble bay, because, in our homeward voyage, we called here a second time, and I shall then have occasion to remark on it" (Darwin, 1839: 11, 12).

Or perhaps on a little less philosophical but very beautiful mode I was reminded of Douglas Botting's words in his book on Alexander von Humboldt, who with his friend Bonpland was the first ever to understand the richness of tropical vegetation. I think this says it very well too.

> "At nine in the morning on 16 July 1799 the *Pizarro* anchored in the Port of Cuminá and even the surviving typhoid victims managed to drag themselves up on deck to have a look. After three weeks on the high seas, the land seemed breathtaking. The high mountains of New Andalusia, half veiled by mists, line the horizon; the town in its fort glimmered between tall coconut palms along the banks of a river; rose-coloured flamingoes, snowy egrets and huge brown pelicans the size of swans foraged along the shore at the edge of a motionless green sea; even at that early hour, the light was dazzling. Humboldt and Bonpland hurried ashore and looked around them. The place bowled them over, instantly and totally. In the first flush of his enthusiasm, Alexander wrote to his brother:
>
> 'What a fabulous and extravagant country we're in! Fantastic plants, electric eels, armadillos, monkeys, parrots: and many, many, real, half-savage Indians.
>
> 'What trees! Coconut palms 50 to 60 feet high; *Poinciana pulcherrima* with a big bouquet of wonderful crimson flowers; pisang and a whole host of trees with enormous leaves and sweet smelling flowers as big as your hand, all utterly new to us. As for the colours of the birds and fishes—even the crabs are sky-blue and yellow!

Figure 8. William Ramirez, an entomologist from the University of Costa Rica, and Gentry on a field trip with leaves of *Gunnera* that are locally used as disposable umbrellas.

Up till now, we've been running around like a couple of mad things; for the first three days we couldn't settle to anything; we'd find one thing, only to abandon it for the next. Bonpland keeps telling me he'll go out of his mind if the wonders don't cease soon.'

"In this exotic new world the explorers seem to have experienced a kind of sensory ecstasy. Nothing—no shape, no form, no voice, no colour, no smell—was familiar to them. Nothing would readily fit into their existing pattern of memory and experience, therefore, everything seemed to demand equal attention. The Indians—*naked!* Their huts—*bamboo and palm leaf!* Their chairs—*branches of coral washed up on the shore!* Their plates—*half a coconut shell!* This way and that they charged, confronted at every turn with brilliant and startling new visions, like men in a mescalin trance—here a *quama* tree loaded with silvery blossoms, there a castle moat full of crocodiles. It required some effort of will to turn their attention to more mundane but necessary matters. For first they had to present their passports to the Governor, and then they had to find somewhere to live" (Botting, 1973: 76).

Al Gentry lived from January 6, 1945 to August 3, 1993. He had a wonderful life. It came to an abrupt and sad end, and when his life ended Al Gentry joined the ranks of other botanists who died through the years in the pursuit of the same kind of knowledge, the same kind of ecstasy that he undoubtedly felt on that day in 1967 when he first plunged into the forest of Costa Rica. Banister in Virginia, Forskåhl in Arabia, Löfling in Venezuela, David Douglas in Hawaii, Jeffery in the Colorado desert, Leitner in Florida, and Orton in Bolivia at Lake Titicaca are among the botanists whom Al now joins who gave their lives in the same quest in which he was engaged. Al brought his enormous energy to learning about plants educating people and about sharing his enthusiasm for them. Tropical plants and tropical nature are the most exuberant expression of biology on earth and it's the part of that expression that it is hardest for us all to understand, most wondrous to us all, and most difficult to deal with. As we have heard, hardship in the field was perfectly acceptable to him and the amenities were always forgotten in his relentless drive for new information and new experience. He really loved his students. We set a rule at the Garden that no one had to teach students, anybody could do exactly what they wanted. For Al there was no choice. He loved dealing with students at Washington University, Saint Louis University, the University of Missouri-St. Louis, and as we have heard all over Latin America. He loved to think about plants and to learn about plants and communities, the relationships between them, the inventories of the biodiversity, the basic information that would make conservation possible. Our loss, which we feel very deeply, is shared by biologists and people who knew him and people who had even a dim understanding of his work from all over the world, and we have received countless messages of condolences, especially from his Latin American colleagues. Among the things that we will be doing in his memory will be the establishment of a fund to support education for Latin American botanists, the Flora of Peru Checklist, which will be published within the next two months will be dedicated to his memory, the first complete inventory of the plants of a South American country. The March issue of *Conservation Biology,* which will have a major article by Oliver Phillips and Al in it, will be dedicated to his memory. The Amazonian ethnobotanical dictionary by Jim Duke and Rodolfo Vásquez which is in press will, as we've heard from Mark Plotkin reading Jim Duke's words, be dedicated to his memory. Along with Conservation International, we will sponsor a symposium or colloquium on Rapid Assessment and publish the results as a contribution to continuing that effort. And here at the Garden, we will find the necessary means to finish his taxonomic work in progress on the Bignoniaceae and other fronts. And to summarize and organize and publish his work on some 250 forest plots, and you have heard about the possibility of dedicating reserves in the memory of Al and Ted Parker.

What does it all mean? Very, very hard to say. I have been wondering about that question for quite some time. I believe deeply and profoundly that one can be happiest if one looks on life and all the subparts of life not as a destination, not as arriving at the destination, but as the journey to that destination. What happens along the way is the whole point. I think about Al growing up in a small Kansas town in the late 1940s, being fascinated by a leaf in the sun or by a butterfly, by a sparrow, or by a little dog, the same sorts of things that anybody growing up in the country would be fascinated by and would feel and note. It is experiences like that when you are a little kid that add up to create your own style. To give you a feeling for what is important to you and what you want to do. What you want to make out of it all. What you want your journey to be like. Each of us has a completely different set of experiences and each of us puts together those experiences in his or her own way and they add up to the kind of person we are, the things that

Figure 9. Gentry pressing and identifying plants on Olaf Hedberg's dining room table. While in Stockholm to receive the Crafoord Prize in 1990, Gentry installed one of his 0.1-ha transects, with Hedberg from the Botanical Museum, at Uppsala University.

we enjoy and the things that allow each of us to make a unique contribution. Listening to those who spoke this morning and thinking about the feelings that we all share, I think we can all be very proud of our botanical family, our biological family, our Missouri Botanical Garden family, the network of people who care about life on earth and want to do something about it, but let's say in a humbler way the network of those of us who care about one another. It should have been crystal clear in thinking about Al's life and in listening to these remarks that the best things in life don't amount to putting on an act for one another or living up to some sort of general expectations about what you should do in order to be able to have perhaps a wonderful eulogy at the end of it all. The best thing in life is living day to day, it's doing it. If we can learn to the extent that each of us makes a unique contribution, to the extent that we can learn to cherish and appreciate the contribution that each one of us make, we will be able to fulfill our own lives best. I don't want to mince words, and the speakers have made it clear that in some respects Al was a difficult person. We are all difficult people. We just have different kinds of difficulty, but the genius is the love that we feel for one another, the cherishing that we can do for one another, the fraying that we can give one another to accomplish great things together and fulfilling things together come from understanding, appreciating, and cherishing even those difficulties. It seems that at a time like this the most appropriate single emotion that we can share is the desire to cherish and love and respect and tolerate one another more. The rewards of that are great and the penalties for not doing that are correspondingly great.

Let's conclude with what Darwin said after spending six months in Brazil. It is true that he did stop again after circumnavigating the globe (remember he was about the same age as Al was when he first got to the tropics), he did stop by briefly on his way home, but it wasn't the big celebration that he expected it to be. So let's hear what he said in conclusion, what Darwin said after six months in Brazil, first time around. The big time, the big experience, the thing that you are doing now is always

the big experience—that's the thing to remember, don't look for some kind of future wonderful thing that is going to make everything all right, just do it. On the 23rd of June in 1832 Darwin said,

> "Again I went to the forest, which so often has been proved so fruitful in all kinds of animals.—It is in all probability the last time I shall ever wander in a Brazilian forest.—I find the pleasure derived from such scenes increases, instead as might have been expected, diminishing. Today instead of the rude tracks, I followed a brook, which in a narrow ravine flowed amongst the huge granitic blocks.—No art could depict so stupendous a scene.—The decaying trunks of enormous trees scattered about, formed in many places natural bridges; beneath & around them the damp shade favoured the growth of the Fern and Palm trees.—& looking upwards the trees in themselves lofty, thus seen, appeared an almost incredible height.—I soon found even by creeping, I could not penetrate the entangled mass of the living & dead vegetation.—On coming out of the forest, the effect without any exaggeration is that of the full light of the sun breaking on a person who has just left a darkened room" (Keynes, 1988: 76).

Our deepest sympathies to Al's family and those he leaves behind. Our shared memories of him will be with us always. I thank you all for coming. I appreciate the wonderful and heartfelt comments by all the speakers on behalf of our sorely missed colleague. Thank you.

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—Peter H. Raven, Director, Missouri Botanical Garden

Exarata chocoensis A. Gentry, Syst. Bot. 17: 503. 1992.

"This remarkable plant seems to be morphologically intermediate between tribe Schlegelieae . . . and tribe Tecomeae." Gentry had been aware of this problematic new genus since at least 1979 but had refrained from describing it for some years "due in part to uncertainty about its familial placement and in part to confusion about whether it is a tree or a climber." Fieldwork conducted in 1991 with a RAP team in eastern Esmeraldas, Ecuador, proved that the plant was a tree and supported its generic segregation from *Schlegelia*. The illustration is by John Myers, who has illustrated hundreds of plants for the Missouri Botanical Garden research effort, and is reproduced with the permission of *Systematic Botany*.

TAXONOMIC REVISION OF *CRUCKSHANKSIA* AND *OREOPOLUS* (RUBIACEAE: HEDYOTIDEAE)[1]

Charlotte M. Taylor[2]

ABSTRACT

Oreopolus is here distinguished based on its ternate leaves, triangular entire to shortly mucronate or bilobed stipules, simple inflorescence bracts that resemble stipules, and calyx lobes that do not enlarge in fruit; thus circumscribed it includes only *O. glacialis* (Poepp.) Ricardi. *Cruckshanksia* is distinguished by opposite to subalternate leaves, erose bilobed stipules, 2–7-lobed inflorescence bracts that resemble the leaves, and calyx lobes that are markedly enlarged in fruit; seven species are recognized here. Keys and complete descriptions, nomenclature, and distributional information are presented.

The taxonomy and study of *Oreopolus* Schltdl. and *Cruckshanksia* Hook. & Arn. (Hedyotideae; Puff, 1988; Robbrecht, 1988) have been closely intertwined since these genera were first described. The type species of *Oreopolus* was first described in *Cruckshanksia,* and two other species, *C. macrantha* Phil. and *C. palmae* Clos, have been alternatively treated in *Oreopolus* by some authors (e.g., Ricardi, 1963a). Both of these genera are endemic to temperate South America and share generally similar habits, corollas, and fruit, including several unusual features, and they appear to be closely related. These plants are characteristic of cool dry sites from near sea level to as high as 3500 m in the northern end of their range. *Cruckshanksia* is found at low to high elevations in arid central to northern Chile, with two species, *C. macrantha* and *C. hymenodon* Hook. & Arn., extending into adjacent Argentina. *Oreopolus glacialis* (Poepp.) Ricardi is found in the Andean Cordillera from central Chile and Argentina south into Tierra del Fuego.

These two genera share papery to membranaceous capsules with loculicidal dehiscence and two ovules per locule, with the ovules borne on an elongated pseudoseptum (Fig. 1A, B). This pseudoseptum is attached peltately to the true septum and extends at right angles from it into the locule. The genera also resemble each other in their low, usually geophytic or cryptophytic habit and distylous flowers with bright yellow salverform corollas with slender tubes. However, *Oreopolus* can be separated by its usually ternate leaf arrangement, entire triangular stipules that are usually imbricate by the poor development of internodes, floral bracts that resemble the stipules, and calyx lobes that do not enlarge markedly in fruit. In contrast, opposite to occasionally subalternate leaf arrangement, erose usually deeply bilobed stipules separated by well-developed internodes, inflorescence bracts that resemble the cauline leaves, and calyx lobes typically enlarging markedly in fruit distinguish *Cruckshanksia.* Additionally, *Cruckshanksia* is distinguished by its inflorescence bracts and in some species cauline leaves that are deeply 2–6-lobed, an unusual feature. Several species are also notable for the prolongation of one or more of the calyx lobes into a stipitate petaloid appendage.

All of the species treated here were first described in *Cruckshanksia,* and were retained in that genus until recently (e.g., Schumann, 1891; Muñoz, 1966). This group was studied in detail by Ricardi (1963a, b, 1968, 1973; Ricardi & Quezada, 1963), who first separated *Oreopolus* with only one species (Ricardi, 1963a). Later Ricardi (1973) restricted *Cruckshanksia* to seven species with well developed petaloid calyx lobe appendages and transferred two species that lack these structures to *Oreopolus.*

GENERIC LIMITS

Regardless of how they are delimited from each other, *Cruckshanksia* and *Oreopolus* share a dis-

[1] I thank several colleagues for valuable comments and helpful discussions, notably M. Muñoz, J. Pipoly, P. Peñailillo, M. Quezada, E. Robbrecht, R. Rodríguez, and S. Teillier, an anonymous reviewer, the editor of *Gayana, Botánica* for permission to use previously published figures, and the curators of the herbaria listed in the taxonomy section for making specimens available. C. von Bohlen, A. Marticorena, and A. Pool were invaluable field companions. Special thanks are due to N. Bacigalupo and C. Marticorena. This work was supported in part by a grant from the National Science Foundation to the Missouri Botanical Garden for the Flora of Chile project (DEB-9201097).

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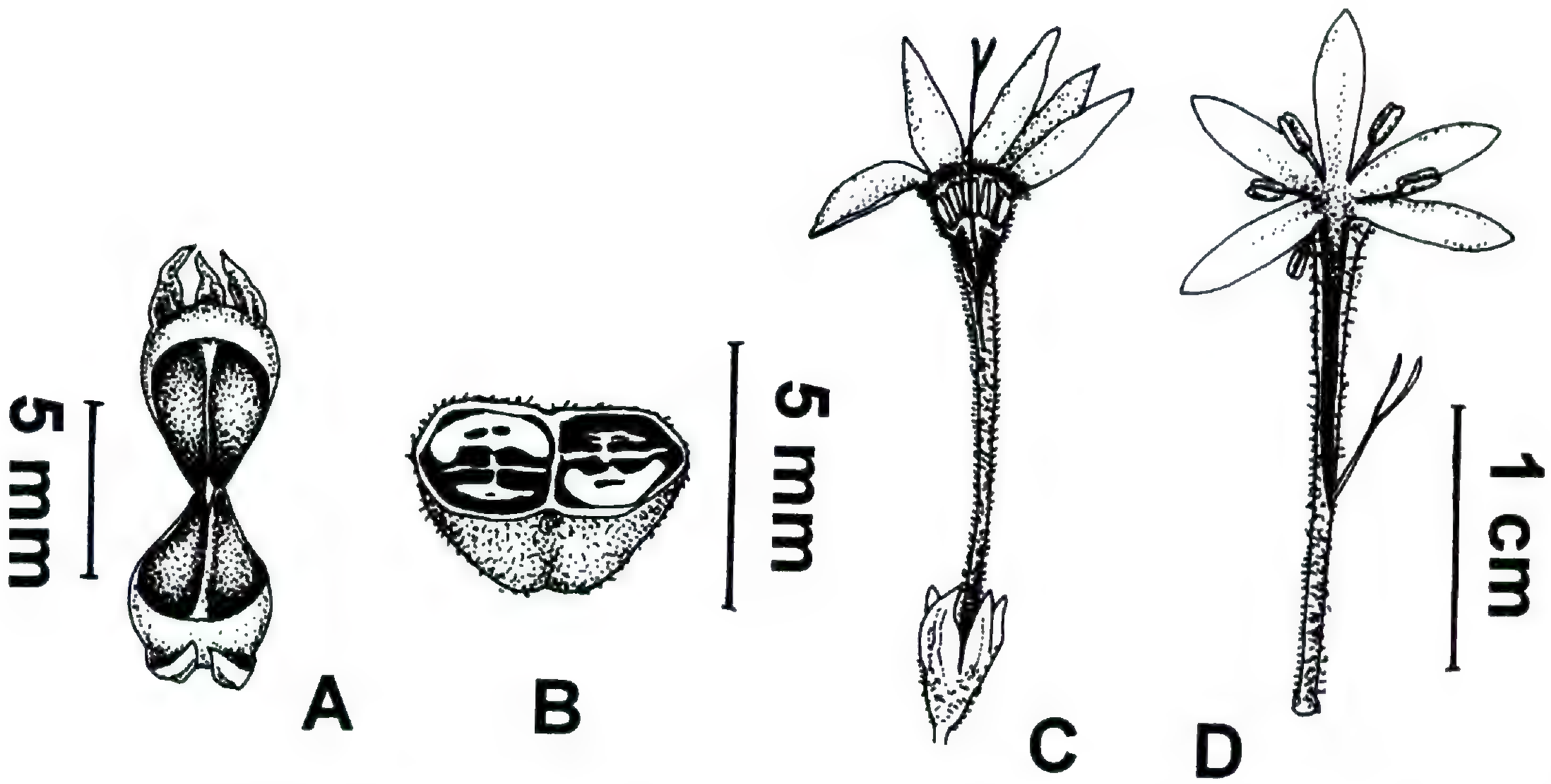

Figure 1. Fruit and floral details of *Oreopolus glacialis*.—A. Dehisced capsule that contained two developed seeds.—B. Cross section of capsule containing two developed seeds.—C. Long-styled flower, partially dissected.—D. Short-styled flower, partially dissected. A, B from Ricardi (1963a: fig. 3C, F); C, D from Ricardi (1963a: fig. 2B, D). C, D to same scale.

tinctive and apparently unique ovary arrangement, as well as distylous flowers with similarly shaped salverform yellow corollas. Based on the ovary arrangement, these genera appear to be closely related.

As circumscribed by Ricardi (1963a), *Oreopolus* included three species and was distinguished by its capsules dehiscent into two valves and flowers lacking petaloid calyx lobe appendages, while *Cruckshanksia* included seven species (two of which are not recognized in the current treatment) and was distinguished by its capsules dehiscent into four valves and flowers each with one or more petaloid calyx lobe appendages (Ricardi & Quezada, 1963; Ricardi, 1963a). However, two species that Ricardi placed in *Oreopolus*, "*O. macranthus*" (*C. macrantha*) and "*O. palmae*" (*C. palmae*), were not known in fruit according to his own descriptions (Ricardi, 1963a), and another species that he placed in *Cruckshanksia*, *C. lithiophila*, is so similar to *C. macrantha* that these can be separated only by the size and shape of the mature calyx lobes. Mature capsules of *C. macrantha* and *C. palmae* are now known. In both species the capsules are dehiscent into four or five valves, which either necessitates the transfer of these two species to *Cruckshanksia* and the separation of the genera only by the number of capsule valves, or, if these species are retained in *Oreopolus*, the separation of the genera only by the presence versus absence of petaloid calyx lobe appendages.

Neither of these alternatives takes into consideration several other unusual features, in particular the ternate leaves and membranaceous stipules of *Oreopolus glacialis* and the 3–7-lobed foliaceous inflorescence bracts found in the remaining species. Although Ricardi's illustration of "*O. macranthus*" (1963a: fig. 5) clearly shows its three-lobed foliaceous inflorescence bracts, this feature was not included in his descriptions of either this species or "*O. palmae*," although it is present in both taxa, nor was it mentioned in the genus description he presented for *Oreopolus*. All of the species studied here except *O. glacialis* also share well-developed calyx lobes that persist and usually enlarge markedly on the fruits, and filamentous erose appendages on the calyx limb and also on at least some of the stipules and inflorescence bracts. These unusual features support the circumscription of an apparently monophyletic group comprised of all the species studied except *O. glacialis*. Therefore, *Oreopolus* is here circumscribed to include one species, *O. glacialis*, while the other two species included in this genus by Ricardi are here assigned to *Cruckshanksia*.

The two species here transferred back to *Cruckshanksia*, *C. macrantha* and *C. palmae*, do not bear petaloid calyx lobe appendages but do share with the other *Cruckshanksia* species relatively large calyx lobes that are narrower at the base than at the middle and are enlarged in fruit, in contrast to the smaller triangular lobes of *Oreopolus*, which are

broadest at the base and do not enlarge at all in fruit. This revised classification also eliminates the problem of placing two very similar species, *C. macrantha* and *C. lithiophila*, in separate genera, even though these are so similar that when they are in flower they cannot always be separated with confidence.

The characters that are used here to distinguish *Oreopolus* from *Cruckshanksia* are summarized in the key to the genera presented in the taxonomic treatment, below. In the following morphological survey, *Oreopolus* and *Cruckshanksia* are compared as they are delimited in the taxonomic treatment.

Morphology of *Oreopolus*

Habit. Plants of *Oreopolus* are perennial hemicryptophytes originating from woody taproots. They form dense low cushions to 75 cm in diameter in open sand or exposed hard soils or rubble.

Stems. The stems are stout and the internodes are usually very shortly elongated at most, usually to less than the length of the stipules, so that these overlap.

Vesture and crystals. The vegetative portions of the plants range from completely glabrous to moderately or sometimes densely puberulous with short unicellular or uniseriate trichomes. The plants contain raphides, although these may be difficult to observe in succulent tissues.

Leaves. The leaves are ternate or rarely opposite, shortly petiolate, simple, and lack domatia. The venation is generally pinnate, although often only the midrib is visible. The cauline leaves are all similar.

The stipules are interpetiolar and fused to the bases of the petioles (Fig. 2A). They are generally triangular in shape, though frequently shortly mucronate or sometimes shortly bilobed at the apex, with entire margins. They are membranaceous and usually nearly hyaline.

Inflorescences. The flowers are terminal and solitary, or terminal and axillary and borne in congested groups of two to six. Each flower is subtended by bracts that resemble reduced stipules, and are triangular, membranaceous, and entire along the margins, but are acute rather than bilobed at the apex. The leaves at the distalmost nodes exceed and usually to some extent enclose the inflorescences.

Flowers. The flowers are hermaphroditic and distylous (Fig. 1C, D). Long-styled and short-styled forms are represented on herbarium specimens in approximately equal proportions, and frequently are found mixed in the same collection when more than one plant was sampled. These forms differ in relative style lengths, point of insertion of the stamens, degree of development of the filaments, and form and pubescence of the corollas. The stigmas are exserted in all mature long-styled flowers seen (in contrast to the apparently delayed elongation of the style in *Cruckshanksia*; see below).

The ovary is inferior and bilocular, turbinate in shape, and pilosulous. Ovary pubescence is not correlated with pubescence of the vegetative parts. Each locule contains two ovules, which are attached to elongated axile placentas that extend perpendicularly from the septum into the locules to form pseudosepta that almost completely subdivide each locule (Fig. 1B). The ovules are anatropous.

The calyx limb may be glabrous or puberulous, and is deeply five-lobed with the lobes generally similar in size and shape. The lobes are triangular to lanceolate, with an acute or sometimes shortly emarginate apex. Colleters have not been seen.

The corollas are salverform with slender cylindrical tubes and five triangular lobes with valvate aestivation. They are pale to usually very bright yellow throughout. The shape of the tube is dimorphic, with the tubes of the short-styled form uniformly cylindrical in contrast to those of the long-styled form, which are swollen for several millimeters at the top to accommodate the included anthers (Fig. 1C, D). This swollen portion of the long-styled form was referred to as the "garganta" by Ricardi and Quezada (1963). The pattern of pubescence is also dimorphic: both the long-styled and short-styled forms are similarly puberulous to pilosulous externally (abaxially) in the tubes and on the lobes, but the short-styled form is glabrous internally (adaxially) throughout the tube while the long-styled form is glabrous in the lower portions of the tube but barbate in the throat.

The five stamens are inserted at the top of the corolla tube in short-styled flowers, and at the base of the throat swelling in long-styled flowers. The anthers of short-styled flowers are exserted on slender, usually flattened filaments, while those of long-styled flowers are subsessile and included. The anthers of both floral forms are narrowly oblong and dehiscent by longitudinal slits.

The style is slender and filiform, in the short-styled form extending to only a little beyond the middle of the corolla tube and in the long-styled form shortly exceeding the corolla tube. The paired stigmas are linear and papillose on the adaxial surface but glabrous on the abaxial surface in both floral forms. The disk is not evident ("not developed," Ricardi & Quezada, 1963, my translation from the Spanish).

Infructescences and fruit. The infructescences do not differ in form from the inflorescences. The fruit is a papery- to chartaceous-walled obovoid capsule that is somewhat flattened laterally. The capsule is dehiscent loculicidally and apparently basipetally into two valves. The calyx limb is persistent on the capsule, frequently becoming split completely between the lobes.

The seeds are planoconvex to somewhat obovoid and somewhat flattened, with a smooth brown to black seed coat. A median sulcus on one side marks the site of attachment to the placenta, and at dispersal some placental material frequently remains attached here. The seeds of *Oreopolus* are similar to those from species of Rubiaceae with only one ovule and seed per locule and two per fruit; however, because the placenta is enlarged perpendicularly to the septum in *Oreopolus* the seeds are borne at right angles to the true septum, so the sulcus is on the lateral face and the true adaxial face is smooth.

Morphology of *Cruckshanksia*

Habit. Plants of *Cruckshanksia* are perennial or sometimes annual geophytes or hemicryptophytes originating from ropelike woody taproots and underground stems with corky, usually red-brown bark, except for those of *C. pumila*, which are typically annuals with a smooth gray to brown epidermis. The perennial plants generally form loose circular clumps to as much as 40 cm in diameter, with the above-ground stems weak to reclining. Most or all stems die back to the ground during dry or cold periods. The annual plants of *C. pumila* may grow to 15 cm tall and branch several times, but may also flower at only 3–4 cm tall, with the flowers produced from the second stem node above the cotyledons. Individual plant size in this species may be correlated with microsite water supply.

Stems. The taproots of the perennial species usually produce four to ten or more separate slender stems. These may be borne above or below ground. Some species, notably *Cruckshanksia macrantha* and *C. lithiophila*, typically have twenty to thirty or more of these stems. Axillary buds are often well developed and frequently densely pubescent.

The above-ground stems are generally slender, with well-expanded internodes. More basal internodes are generally quadrate while those at more distal nodes are subterete to irregularly angled or channeled. Although Ricardi and Quezada (1963) used the relative lengths of the more proximal internodes to distinguish species, this character appears to vary with local environmental conditions and is not considered taxonomically reliable here.

Vesture and crystals. Plants of *Cruckshanksia* are generally puberulent to densely villosulous or shortly pilosulous, with short unicellular or uniseriate trichomes found on most or all parts of the plant distal to the hypocotyl. The plants contain raphides.

Leaves. The cauline leaves are opposite or occasionally subopposite to alternate at more distal nodes, and lack domatia. The venation is generally subpalmate, with one to two pairs of strongly ascending secondary veins arising in the basal third or half of the blade. In species with very narrow leaf blades (*Cruckshanksia verticillata, C. montiana*), only the midrib may be evident and sometimes even this cannot be distinguished. In annual plants of *C. pumila*, the cotyledons are usually persistent on the flowering and sometimes also the fruiting plants.

The cauline leaves at the more basal nodes are simple or they may be deeply two- to three-lobed in some individuals of *Cruckshanksia verticillata*. The leaves of more distal nodes may be consistently simple and distinct from the lobed "floral leaves" or foliaceous inflorescence bracts ("hojas florales" and "pseudotrifolios" sensu Ricardi and Quezada, 1963) in *C. palmae, C. macrantha*, and *C. lithiophila*, or in the remaining species the cauline leaves at the upper stem nodes may vary from simple to lobed and intergrade with the floral bracts. Simple leaves taper to an acute, usually short-petiolate base; the lobed leaves are cuneate to rounded at base and sessile to subsessile. The lobed cauline leaves of several species (notably *C. montiana* and *C. hymenodon*) often bear linear multicellular appendages on the margins near the bases of the lobes, and sometimes in the sinuses between the lobes. These structures were apparently referred to as "escamas" by Ricardi and Quezada (1963), and are perhaps comparable to the erose marginal projections found on the stipules (see below).

Stipule morphology typically varies on an individual plant. At more basal nodes bearing simple leaves and at the cotyledon-bearing nodes of annual plants, the stipules are interpetiolar and may be free or fused to the petioles (Fig. 2B). The interpetiolar portion may be triangular or shortly bilobed, and entire or somewhat erose. At progressively more distal nodes, the stipules typically are progressively more deeply bilobed and more erose, with the linear marginal appendages up to several millimeters long (Figs. 2C, E). At stem nodes closest to the inflorescence, the stipules are sometimes completely divided into two lobes, which may be

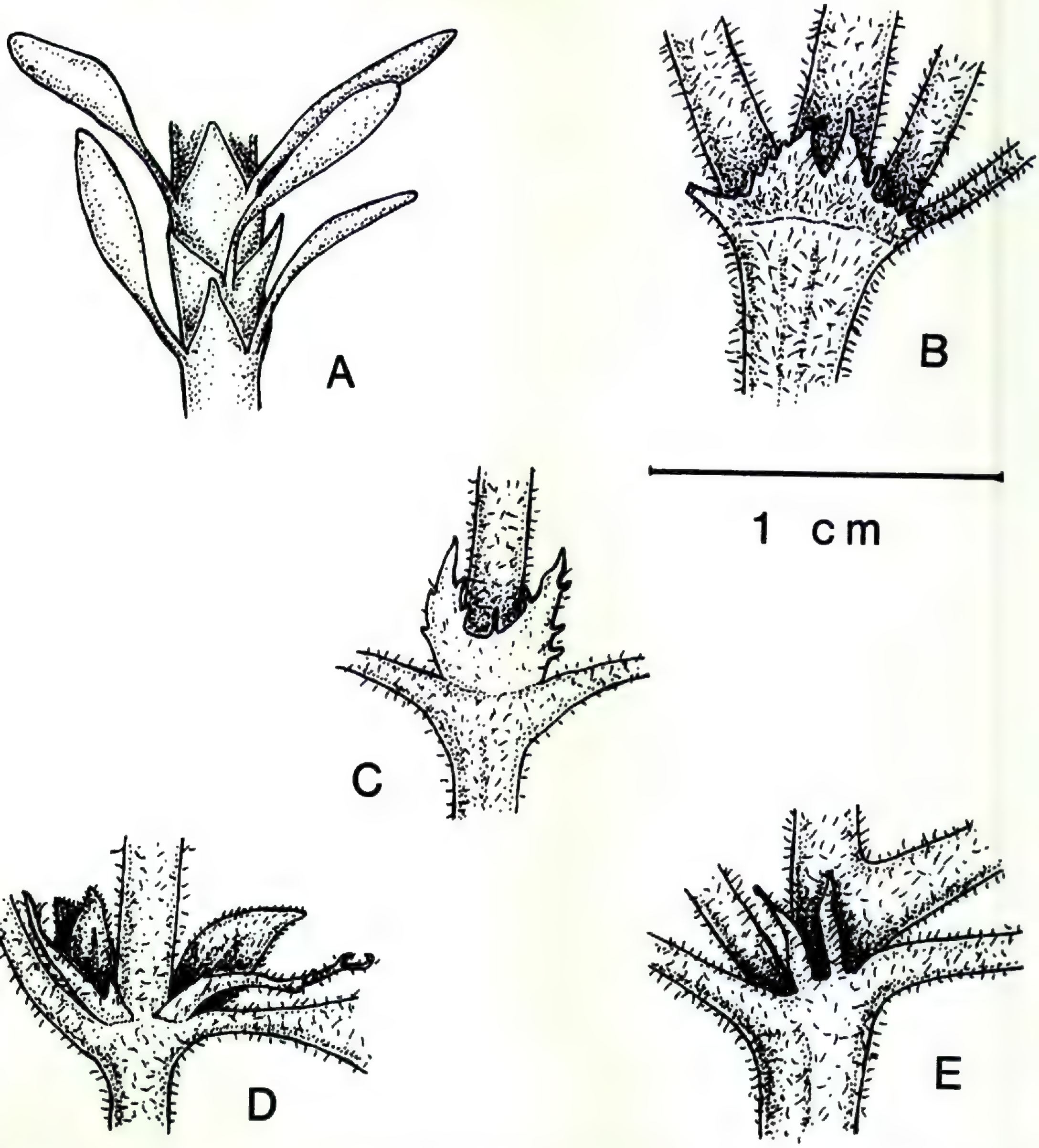

Figure 2. Stipule morphology of *Oreopolus* and species of *Cruckshanksia*. —A. *O. glacialis*, node near middle of stem. —B. *C. hymenodon*, node near base of stem. —C. *C. montiana*, node mear middle of stem. —D. *C. hymenodon*, node immediately below inflorescence. —E. *C. hymenodon*, node near middle of stem. All to same scale. A based on *Donat 172*, MO; B, E based on *Taylor 10782*, MO; C based on *Gay s.n.*, MO-393317; D based on *Taylor 10781*, MO.

connected by an interpetiolar line or may show no connection at all (Fig. 2D). These lobes are frequently fused to the petioles, and typically have strongly erose margins. In several species (notably *Cruckshanksia hymenodon* and *C. pumila*), the stipules of distal stem nodes are often irregular: only one lobe on one side may be developed, or one lobe may be well developed and free while the other lobe is reduced and fused to the leaf. Irregularly lobed cauline leaves are subtended by irregular stipules, and three-lobed cauline leaves lack stipule lobes. Ricardi and Quezada (1963) used degree of stipule lobing to distinguish species, but this feature seems to vary with developmental stage on an individual plant, and several degrees of lobing are typically found on a single stem. This feature is not considered taxonomically reliable here.

The correlation between irregular stipule development and lobed leaf shape suggests that the lobed leaves could be formed by a fusion of expanded stipule lobes and the leaf blade, as in *Galium* L. and some Knoxieae (Robbrecht, 1988). In

this case the lateral leaf lobes would be equivalent to expanded stipule lobes. This possibility is supported by the lack of stipule lobes subtending these leaves, and their sessile rather than petiolate bases. The linear appendages on lobed leaves would then be equivalent to the erose projections characteristic of the stipule margins. More detailed study is needed to evaulate this possibility.

Inflorescences. The inflorescences are terminal, dichasial to somewhat irregular, strongly congested to subcapitate cymes. The flowers are sessile to subsessile (Fig. 3A). Ricardi and Quezada (1963) reported that the flowers of *Cruckshanksia montiana* are borne on pedicels to 2 mm long, but the structures they measured are similar to those they called inflorescence branches in other species, and are considered inflorescence branches here.

Each flower is subtended by an unlobed or usually three- to seven-lobed "floral leaf" or foliaceous inflorescence bract that encloses the flower bud until anthesis (Fig. 3A, B). These structures have been variously referred to as leaves or bracts by different authors; they are here considered bracts based on their position, subtending the individual flowers of a cymose inflorescence, and usually different form from the cauline leaves. This interpretation agrees with that of Jansen (1979) for *Kajewskiella* Merr. & Perry, in which inflorescence bracts are frequently subopposite or alternate and bear colleters. Jansen considered these bracts to be homologous to leaves, although with the problem that colleters, which are typically found on inflorescence bracts of *Kajewskiella,* are normally found on stipules but not leaf blades or petioles. The presence of colleters in the inflorescence bracts of *Cruckshanksia* suggests that not only are the bracts generally homologous to leaves, but that they are homologous to the entire leaf, including the stipules, as proposed also for *Gaertnera* Lam. (van Beusekom, 1967).

The inflorescence bracts of *Cruckshanksia* are generally similar in color, size, and pubescence to cauline leaves, and in those species that occasionally have lobed cauline leaves (notably *C. hymenodon* and *C. pumila*), leaves and bracts may intergrade (see above).

Flowers. The flowers are hermaphroditic, and are distylous in all species of *Cruckshanksia.* (Although Ricardi & Quezada (1963) reported that several species had only one floral form, both have now been found for all species.) Long-styled and short-styled forms are represented in living populations of *C. pumila* and *C. hymenodon* (pers. obs.) and in herbarium specimens of all species in approximately equal numbers. The forms differ in relative style length, point of insertion of the filaments, and form of the corolla. In long-styled flowers the style apparently elongates after anthesis; this one floral form may have a stylar or "ixoroid" pollen presentation mechanism (Robbrecht, 1988), which implies that these flowers are also protandrous. The presence of this mechanism has not previously been seen in distylous flowers and must be confirmed by field study, but such a mechanism is suggested by the pilosulous pubescence on the uppermost portion of the style and abaxial stigma lobes, to which pollen grains are found adhering in most herbarium specimens that have the style elongated and the stigmas exserted.

The ovary is inferior and bilocular, turbinate or somewhat ovoid or obovoid, and usually relatively densely pubescent. The ovary and ovules are similar to those of *Oreopolus* (see above).

The calyx limb is pubescent similarly to the vegetative portions of the plant, and deeply to nearly completely divided with a tube portion 1.5 mm long or shorter. Calycine colleters have not been seen. In some species (*C. palmae, C. macrantha, C. lithiophila*), the calyx lobes are consistently five, equal or nearly so, and elliptic to oblanceolate (*C. palmae, C. macrantha*) or slightly to strongly stipitate with the upper portion expanded into a narrowly elliptic to ovate appendage (*C. lithiophila*). In the remaining species the calyx lobes vary from two to five per flower on a single plant, and are usually strongly unequal (Fig. 3A). In these species each flower bears one to four stipitate, appendaged, bright yellow or pink petaloid calyx lobes along with usually one or more shorter triangular lobes, and sometimes also one or more elliptic to oblanceolate lobes similar to the lobes of the inflorescence bracts (these last structures were not described by Ricardi & Quezada, 1963). These petaloid calyx lobe appendages were variously referred to as "sépalos petaloides" and "uñas" by Ricardi and Quezada (1963). The calyx typically also bears erose or linear appendages in the sinuses between the lobes (referred to as "escamas calicinales" by Ricardi & Quezada). These are similar to the erose appendages found on the bracts and stipules.

Strongly and irregularly unequal calyx lobes are found in several genera of Rubiaceae (e.g., *Rondeletia* L., *Pentas* Benth.), and stipitate calyx lobe appendages are also known from other genera of this family (e.g., *Mussaenda* L., *Warszewiczia* Klotszch, *Pogonopus* Klotszch). Such appendages are often brightly colored and are thought to function in attracting pollinators, in which case they are considered semaphylls (Robbrecht, 1988). The ap-

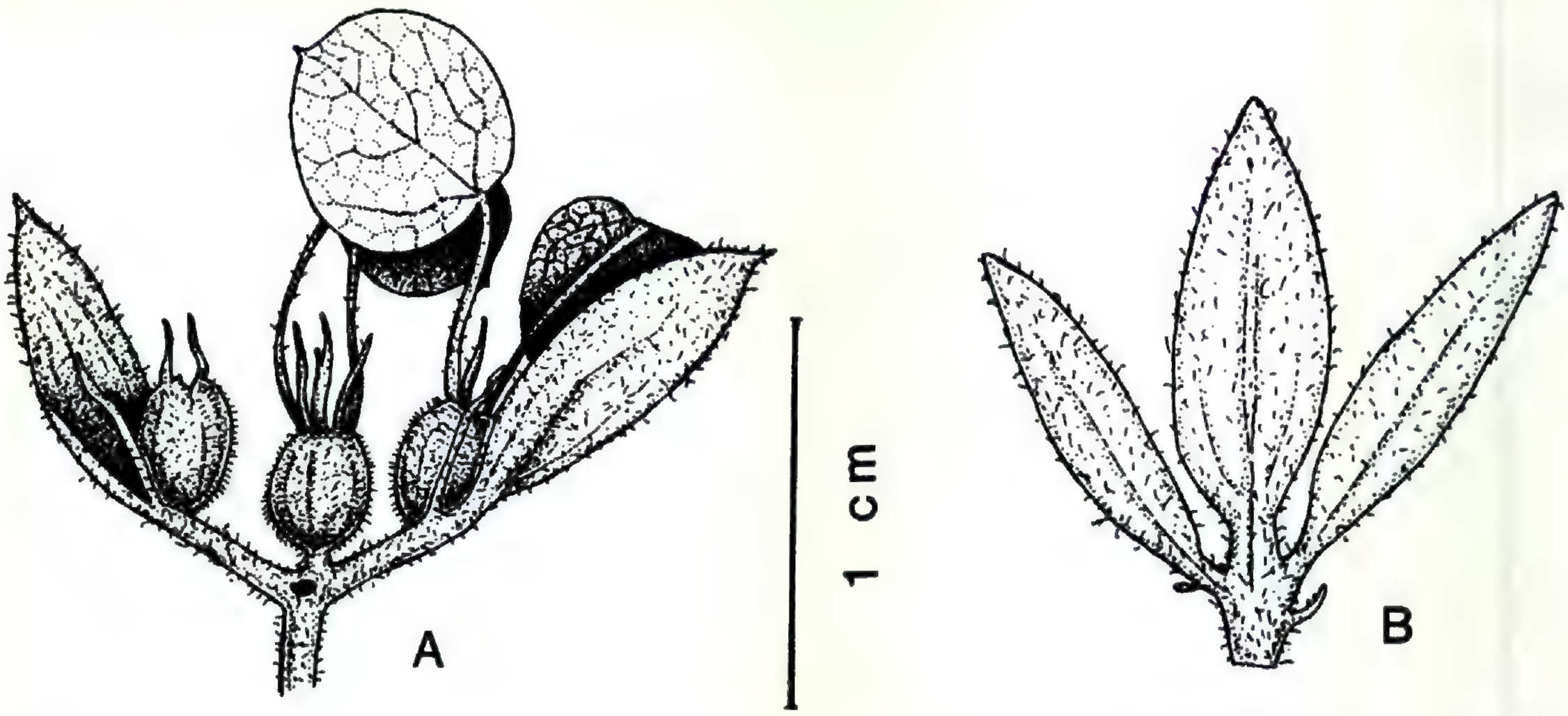

Figure 3. Inflorescence details of *Cruckshanksia hymenodon.*—A. Cymule with immature capsules.—B. Floral bract. Both to same scale. A based on *Mahu s.n.*, MO-3272960; B based on *Wagenknecht 18484*, MO.

pendages found in *Cruckshanksia* are membranaceous, reticulately veined, and generally yellow, or pink to occasionally white in *C. hymenodon.* The form of the appendages changes markedly during development of the flower. In bud they are narrowly elliptic and acutely to obtusely angled at both apex and base. At anthesis in most species they are ovate or elliptic-oblong and rounded to truncate at the base and apex or with a triangular projection and short mucro at the apex. In some species the calyx lobe appendages continue to enlarge markedly as the fruit develops (see below). Previously published descriptions of most *Cruckshanksia* species include measurements of fruiting rather than flowering calyx lobe appendages, probably because the plants usually flower and fruit concurrently and the appendages are larger and more striking in fruit.

Ricardi and Quezada (1963) used the shape of the petaloid calyx lobe appendages to distinguish species. However, this feature is variable, and at best seems to distinguish only developmental stages of an individual flower. Material cited by them frequently shows both of the conditions they used to separate a pair of species on different flowers of the same plant, and this feature is not considered taxonomically reliable here.

The corollas of *Cruckshanksia* are similar in form to those of *Oreopolus* (see above). They are bright to deep yellow and frequently marked with darker yellow on the lobes. The corollas of both floral forms are glabrous internally and on the adaxial surfaces of the lobes, and typically pubescent throughout the external (abaxial) surface. Herbarium specimens of some species, notably *Cruckshanksia hymenodon,* show marked variation in corolla length; this may be real morphological variation, perhaps due to water availability, or it may include differential shrinkage during preparation of dried specimens.

The stamens, style, and stigma are similar to those of *Oreopolus* (see above).

Infructescences and fruit. The infructescences are similar to or often somewhat more expanded than the inflorescences, with the cyme branches elongating to separate the developing fruits (Fig. 3A). The fruit is a papery- to chartaceous-walled, subglobose to ovoid or oblong capsule. The capsule is dehiscent loculicidally, acropetally, and frequently irregularly into two to five valves. In species with variously two to four appendaged calyx lobes, the number of capsule valves often equals the number of appendaged calyx lobes. The illustration presented by Schumann (1891) suggests that the dehiscence is basipetal, but this probably was drawn from a specimen and based on a capsule that was crushed during the drying process; similar capsules can be found on specimens that also have capsules dehiscing from the base. The placentas appear to become fleshy as the capsule matures, and may sometimes be dispersed with seeds still attached.

The calyx limb is persistent on the capsule, and the calyx lobes typically enlarge and sometimes also change shape as the fruit matures. In species in which the calyx lobes are all similar, the lobes typically retain their general shape but become enlarged and papery, and sometimes more strongly narrowed at the base. In species in which the calyx lobes are unequal, the smaller lobes do not change noticeably but the appendaged lobes may enlarge and change form markedly, typically becoming sub-

orbicular to reniform, cordate at the base, and emarginate at the apex, with the triangular apex and mucro becoming inrolled or reduced. At maturity, these appendages are dry, papery, and usually brown, and may function in dispersal or at least dehiscence of the fruit; such structures are considered pterophylls (Robbrecht, 1988).

The seeds are similar to those of *Oreopolus* (see above), except the seed coat may be smooth to rugose.

Taxonomic Treatment

This work is based on study of herbarium specimens from A, BAB, CONC, CORD, CTES, E, F, GH, K, LP, M, MO, NY, SGO, SI, and UC, and field observations in northern Chile in 1991 and 1993. Measurements given in brackets are taken from Ricardi (1963a, 1963b) and Ricardi and Quezada (1963) but were not observed on specimens studied.

Key to the Genera

1a. Leaves ternate or rarely opposite, thickly succulent drying coriaceous; stipules triangular, entire to shortly mucronate or bilobed, closely set or usually imbricated by the limited development of the internodes; leaves drying coriaceous, ternate or rarely opposite; flowers subtended by triangular membranaceous bracts smaller than but similar to the stipules; calyx lobes 5, triangular, never prolonged into petaloid appendages, not enlarging in fruit; corolla pubescence dimorphic, differing in long-styled and short-styled forms; capsules basipetally dehiscent into 2 valves ..... *Oreopolus*

1b. Leaves opposite or sometimes subopposite to alternate at more distal nodes; stipules triangular or shallowly to completely bilobed, entire to strongly erose, separated by elongated internodes; leaves drying chartaceous to subcoriaceous, opposite or sometimes subopposite to alternate at more distal nodes; flowers subtended by simple to usually 3–7-lobed foliaceous bracts similar to the cauline leaves; calyx lobes 2–5(6), elliptic to obovate, subulate, or sometimes prolonged into stipitate petaloid appendages, usually enlarging in fruit; corolla pubescence similar in long-styled and short-styled forms; capsules acropetally dehiscent into 2–5 valves ..... *Cruckshanksia*

Oreopolus Schltdl., Linnaea 28: 493. 1857. TYPE: *Oreopolus citrinus* Schltdl. [= *Oreopolus glacialis* (Poepp.) Ricardi].

Perennial, rather succulent, hemicryptophytic low shrubs from a woody taproot, glabrous to pubescent, with raphides; stems quadrate to terete, internodes usually not or only shortly expanded. *Leaves* ternate or rarely opposite, simple, shortly petiolate; *blades* elliptic to lanceolate, thickly succulent, drying coriaceous, without domatia; venation pinnate but usually not evident; *stipules* interpetiolar, fused to petioles, imbricated by poor development of the internodes, membranaceous, triangular, entire to shortly mucronate or bilobed. *Inflorescences* terminal, capitate, sessile; *flowers* 2–6, distylous, each subtended by a bract resembling a reduced stipule, this sometimes deeply divided with age; *hypanthium* turbinate; *ovary* inferior, bilocular, ovules 2 per locule, anatropous, borne on placentas attached to septum and prolonged into a partial pseudoseptum; *calyx* limb deeply 5-lobed, lobes equal, generally triangular; *corolla* slenderly salverform, yellow, in short-styled form the tube glabrous internally and uniformly cylindrical, in long-styled form the tube swollen and barbate at top, lobes 5, triangular to lanceolate, acute, valvate; *stamens* 5, in short-styled form inserted at top of corolla tube, exserted, with flattened filaments, in long-styled form inserted at base of enlarged throat of corolla tube, included, subsessile, anthers in both forms basifixed, narrowly ellipsoid to oblong, dehiscent by longitudinal slits; *styles* filiform; stigmas 2, linear, papillose, in short-styled form borne near middle of corolla tube and abaxially glabrous, in long-styled form exserted by several mm and abaxially pilosulous; disk rudimentary. *Fruits* capsular, obovoid, laterally somewhat flattened, papyraceous to chartaceous, dehiscent loculicidally and basipetally into 2 valves, calyx limb persistent, similar to that of flowers; *seeds* planoconvex to obovoid, somewhat compressed, sulcate at attachment, brown, smooth to somewhat rugose.

One species of dry cool regions in the Andean Cordillera, central Chile and Argentina to Tierra del Fuego.

Oreopolus glacialis (Poepp.) Ricardi, Gayana 6: 7. 1963. *Cruckshanksia glacialis* Poepp., in Poepp. & Endl., Nov. Gen. Sp. 3: 31. 1841. TYPE: Chile. IX Region.[3] Prov. Malleco: Volcán Antuco, 8500 ft. [2750 m], Mar. 1829, *Poeppig 59* (holotype, B not seen, destroyed; isotype, CONC–28779).

Oreopolus citrinus Schltdl., Linnaea 28: 492. 1857. TYPE: Chile. X Region. Prov. Valdivia: "Cordillera de Ranco, in tierra Pehuelchorum," Dec. 1854, *Lech-*

[3] For map of regions in Chile see *Flora de Chile*, Vol. 1, edited by Clodomiro Marticorena and Roberto Rodríguez, published in 1995 by Universidad de Concepción, Chile.

ler/Hohenacker 2895 (holotype, HAL not seen; isotypes, CONC, K, NY, photo (neg. #2479) SGO).

Oreopolus patagonicus Speg., Rev. Fac. Agron. Veterin. La Plata 3(30–31): 525. 1897. *Cruckshanksia patagonica* (Speg.) Macloskie, Rep. Princeton Univ. Exp. Patagonia 8(5): 740. 1905. TYPE: Argentina. Prov. Santa Cruz: San Julián, río Deseado, 1899, *C. Ameghino s.n.* (holotype, LP not seen; isotypes, CONC–28803, F–657367).

Oreopolus glacialis var. *pilosus* Ricardi, Rev. Fac. Ci. Agrar. 13(1–2): 4. 1968. TYPE: Argentina. Prov. San Rafael: Alto Valle del Atuel, Quebrada del Arroyo Nield, 3100 m, 9–17 Jan. 1954, *A. Ruiz Leal 15678* (holotype, herb. H. Ruiz Leal, not seen; isotype, CONC).

Plants forming dense lawns or cushions to 75 cm diam., glabrous or moderately to densely puberulous, usually 3–8 times branched, from taproots to 15 mm thick, with red somewhat corky bark; stems 2–10(20) cm long, suberect. *Leaves* with petioles 2–7 mm long; *blades* 8–15 mm long, 2–6 mm wide, at apex acute, at base acute to rounded; *stipules* 1–3 mm long, smooth to somewhat costate, acute to mucronate or bilobed with mucro or lobes to ca. 0.5 mm long. *Inflorescences* ca. 1 cm long and wide excluding corollas; *flowers* with hypanthium 1–2 mm long, pilosulous; *calyx* limb membranaceous, glabrescent, (1)3–4 mm long, divided for ¼–½, lobes (0.5)1–2 mm long and wide, triangular to lanceolate, acute to emarginate or shortly bilobed; *corolla* pale to bright yellow, puberulous to pilosulous externally (abaxially), tube 13–16 mm long, 0.3–0.5 mm diam. near middle, enlarged throat of long-styled form 1.5–2 mm long and in diam., lobes 4–5.5 mm long, 1–1.5 mm wide at base; *anthers* 1–1.5 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 0.3–0.5 mm long, in long-styled form exserted by 1–5 mm. *Capsules* 5–8 mm long, 3–6 mm wide, pilosulous; *seeds* 4–6 mm long, 2–3 mm wide. Illustration: Ricardi (1963a: fig. 3).

Distribution and habitat. Southern Andean Cordillera, central Chile and Argentina to Tierra del Fuego (32°–53°S), at 2500–3500 m in the northern part of its range, to as low as 300 m in the southern part, usually in open sand, rubble, or hard soil. Collected in flower October through March, in fruit December through March.

The leaves and stems of *Oreopolus glacialis* range from smooth to markedly papillose, with enlarged epidermal cells, throughout its range. In general, surface texture is correlated with plant size: plants with relatively small leaves and short internodes are usually smooth, while those with relatively large leaves and expanded internodes are papillose. No geographic pattern or correlation with other characters is evident for plant size, which probably varies primarily with microhabitat.

The unpublished names "Cruckshanksia oblonga F. Meigen," "Conchospermum oblongum Phil.," "Conchospermum ovatum Phil.," "Conchospermum nudicaulis Phil.," "Oreocaryon nivalis Kuntze ex K. Schum.," "Oreopolus oblonga Phil. ex F. Meigen," and "Oreopolus oblongus Phil." have all been used for *Oreopolus glacialis*. Although some of these names have been listed in synonymy with *Oreopolus glacialis* in previous treatments, none of them has been validly published.

Ricardi originally separated variety *pilosus* Ricardi from the typical variety by its "leaves pubescent on both sides, without glandular punctations," in contrast to the "leaves glabrous with brown glandular punctations abundant on the lower surface" of variety *glacialis* (Ricardi, 1973: 218; my translation from the Spanish text). Occasional plants of *Oreopolus glacialis* from throughout its range are pubescent on vegetative parts with trichomes 0.1–0.2 mm long, and these seem to be the plants that Ricardi intended to segregate as variety *pilosus*. No difference is evident in the density, character, and distribution of pubescence on flowers and fruits of plants he placed in the two varieties. All of the representatives of "var. *pilosus*" were collected near San Carlos de Bariloche in southern Argentina, where vegetatively glabrous plants have been collected apparently sympatrically (e.g., *Buchtien s.n.*, CONC). The structures that Ricardi (1963a) described as "glandular punctations" are found on occasional specimens from throughout the range of this species. These structures may be found on glabrous or pubescent plants, on only the abaxial leaf surface, on both surfaces, or throughout the vegetative parts of the plant. They do not appear to be actual glands, but rather the collapsed walls of enlarged epidermal cells, and are found only on specimens with a markedly papillose epidermis.

However, some plants from near Bariloche, including the type collection of variety *pilosus*, are unusual in having a reduced calyx limb, ca. 1 mm long (e.g., *Boelcke 10049*). This feature was not cited by Ricardi as distinctive, but does seem to be locally frequent in the populations that Ricardi intended to separate in his variety. This variety is not recognized here, though further study may support its separation (N. Bacigalupo, pers. comm.).

Representative specimens examined. ARGENTINA. **Chubut:** Departamento Languiñeo, 50 km al S de Tecka, *Correa et al. 10390* (BAB). **Mendoza:** San Carlos, Laguna Diamante, *Boelcke et al. 10049* (BAB). **Neuquen:** Departamento Minas, Huingancó, La Rinconada, *Correa et al. 9992* (BAB). **Río Negro:** Parque Nacional Nahuel Huapi,

subida al Granito, *Boelcke & Correa 5936* (BAB). **Santa Cruz:** Deseado, Picada Río Deseado-Bahía Nodales, *Correa & Nicora 3443* (BAB). **Tierra del Fuego:** Estancia Sarmiento, foothills to N of Sierra Beauvoir, *Goodall 4380* (BAB, MO). CHILE. METROPOLITAN REGION. **Prov. Cordillera**: Paso de los Peladeros, Jan. 1933, *Grandjot & Grandjot s.n.* (CONC, GH), Feb. 1937, *Grandjot s.n.* (MO–1160900). VI REGION. **Prov. Colchagua**: Cordillera Inguiririca, *Pirion 79* (CONC, GH). VII REGION. **Prov. Curicó**: borders of Lake Planchon, *Zöllner 8455* (MO), *9696* (MO). **Prov. Talca**: entre Paso Pechuneches y Laguna del Maule, *Ricardi et al. 980* (CONC). VIII REGION. **Prov. Biobío**: faldeos de Volcán Antuco, 5.5 km al S del Refugio de Sky, *Stuessy & Baeza 11092* (CONC). IX REGION. **Prov. Malleco**: Volcán Loquimay, *Sparre & Constance 10936* (CONC). XI REGION. **Prov. Aisén**: Río Cisnes, *Ricardi & Matthei 515* (CONC). XII REGION. **Prov. Magallanes**: Estancia Penitente, Río Penitente, near bridge crossing river to E of St. Palermo, *Moore 2264* (BAB). **Prov. Ultima Esperanza**: Las Cumbres, Baguales, *Ricardi & Matthei 378* (CONC).

Cruckshanksia Hook. & Arn., Bot. Misc. 3: 361. 1833, nom. cons., not *Cruckshanksia* Miers, Trav. 2: 529. 1826, Iridaceae, Type = *Cruckshanksia graminea* Miers; not *Cruckshanksia* Hook., Bot. Misc. 2: 211. 1831, Geraniaceae or Ledocarpaceae, Type = *Cruckshanksia cistiflora* Hook. [= *Balbisia peduncularis* (Lindl.) D. Don]. TYPE: *Cruckshanksia hymenodon* Hook. & Arn.

Rotheria Meyen, Reise um die Erde 1: 402. 1834. TYPE: *Rotheria lanceolata* Meyen (= *Cruckshanksia hymenodon* Hook. & Arn.).

Annual or perennial herbs or shrubs, usually geophytic or hemicryptophytic from a woody taproot, glabrescent to usually pubescent, with raphides; stems quadrate to subterete or irregularly channeled, internodes generally expanded; cotyledons usually persistent and photosynthetic on annual plants of *C. pumila*. *Leaves* opposite or sometimes subopposite to alternate at more distal nodes, simple or sometimes deeply 2–3-lobed, shortly petiolate to subsessile; *blades* elliptic to narrowly so, without domatia; venation subpalmate with 1–2 pairs of strongly ascending secondary veins or sometimes not evident; *stipules* interpetiolar, free or fused to petioles or leaf bases, on more basal nodes generally triangular to shortly bilobed with margins entire to shortly erose, on more distal nodes more deeply to completely bilobed with margins erose, the erose appendages sometimes elongate ("escamas" sensu Ricardi & Quezada, 1963) or the stipules reduced or absent when leaves lobed. *Inflorescences* terminal, congested-cymose to subcapitate, branched (0)2–8 times; *flowers* (1)3–15, distylous, subsessile, each subtended by a foliaceous bract, these simple to deeply 3–7-lobed, similar to cauline leaves in size, texture, color, and venation, sessile, deeply 3–7-lobed, entire to erose with prolonged linear appendages; hypanthium cylindrical to turbinate or subglobose, densely pilosulous to villous; *ovary* inferior, bilocular, ovules 2 per locule, anatropous, borne on placentas attached to septum and prolonged into a partial pseudoseptum; *calyx* limb deeply 2–5(6)-lobed, lobes often erose with linear appendages ("escamas calicinales" sensu Ricard & Quezada, 1963), equal (*C. macrantha, C. palmae, C. lithiophila*) or strongly unequal (remaining species), narrowly triangular to elliptic or sometimes prolonged into a stipitate petaloid appendage, this elliptic to ovate, membranaceous, reticulate-veined, puberulent to glabrescent, brightly colored (semaphylls; "uñas," "sépalos petaloides" sensu Ricardi & Quezada, 1963); *corolla* slenderly salverform, bright to deep yellow, externally (abaxially) puberulent to pilosulous, internally glabrous, in short-styled form the tube uniform, in long-styled form the tube swollen at top ("garganta" sensu Ricardi & Quezada, 1963), lobes 5, triangular to lanceolate, acute, valvate; *stamens* 5, in short-styled form inserted at top of corolla tube, exserted, with flattened filaments, in long-styled form inserted at base of enlarged throat of corolla tube, included, subsessile, anthers in both forms basifixed, narrowly ellipsoid-oblong, dehiscent by longitudinal slits; *styles* filiform; stigmas 2, linear, papillose adaxially, pilose abaxially, in short-styled form borne near middle of corolla tube, in long-styled form exserted by several mm; disk rudimentary. *Infructescences* sometimes somewhat more expanded and open than inflorescences but otherwise similar; *fruits* capsular, subglobose to ellipsoid-oblong or ovoid, somewhat didymous, papyraceous to chartaceous, dehiscent loculicidally, acropetally, and often irregularly into 2–5 valves, calyx persistent, often enlarging, with petaloid appendages (pterophylls) becoming ovate or orbicular to reniform, rounded to truncate or emarginate at apex, rounded to usually cordate at base, dry, papery, whitened to yellowed or brown; *seeds* ellipsoid to ovoid, somewhat compressed, sulcate at attachment, brown to black, smooth to verrucose.

Seven species of arid regions from the Pacific coast to the Andean Cordillera in northern Chile, two species (*Cruckshanksia hymenodon, C. macrantha*) extending into adjacent Argentina.

KEY TO SPECIES OF *CRUCKSHANKSIA*

1a. Calyx lobes equal, none bearing petaloid appendages or all lobes bearing them, elliptic to oblanceolate or with stipitate elliptic to ovate blades or appendages in flower, these sometimes becoming orbicular to broadly elliptic in fruit.
  2a. Leaf blades 15–40 mm long, sharply acute at apex; stipules 1.5–2 mm long; calyx lobes in flower 10–15 mm long, in fruit 12–23 mm long, without stipes ..... 1. *C. palmae*
  2b. Leaf blades 8–20 mm long, obtuse to rounded at apex; stipules 0.8–6 mm long; calyx lobes in flower 3.5–11 mm long, including stipe when present, in fruit 7–17 mm long, elliptic to oblanceolate, and without stipes or 9–13 mm long, ovate, and with stipes 10–15 mm long.
    3a. Calyx lobes elliptic to oblanceolate, without stipes, in flower 3.5–5 mm long, in fruit 7–17 mm long ..... 2. *C. macrantha*
    3b. Calyx lobes in flower composed of stipes 3–6 mm long each bearing an elliptic to ovate appendage 3–5 mm long, in fruit the stipes 10–15 mm long with appendages ovate, 9–13 mm long ..... 3. *C. lithiophila*
1b. Calyx lobes unequal, 1–3(4) bearing petaloid appendages, these orbicular to broadly elliptic in flower, and the remaining (0)1–4 lobes elliptic to narrowly triangular or subulate.
  4a. Plants annual or rarely apparently perennial; corolla lobes 1–2.5 mm long; corolla tube 0.1–0.3 mm diam. near middle ..... 5. *C. pumila*
  4b. Plants perennial; corolla lobes 2–4.5 mm long; corolla tube 0.3–1 mm diam. near middle.
    5a. Petaloid calyx appendages pink or white (frequently drying yellow); leaves 2–9.5(15) mm wide ..... 4. *C. hymenodon*
    5b. Petaloid calyx appendages yellow; leaves 0.8–4(6) mm wide.
      6a. Cauline leaves simple or sometimes 3-lobed; petaloid calyx lobe appendages 6–10 mm long and 8–15 mm wide in flower, to 12 mm long and 18 mm wide in fruit ..... 6. *C. montiana*
      6b. Cauline leaves simple to usually 2–3-lobed; petaloid calyx lobe appendages 3–6 mm long and 2–7 mm wide in flower and fruit ..... 7. *C. verticillata*

1. Cruckshanksia palmae Clos, in Gay, Fl. Chil. 3: 194. 1848. *Oreopolus palmae* (Clos) Ricardi, Gayana, Bot. 6: 12. 1963. TYPE: Chile. IV Region. Prov. Coquimbo: "cerros arenosos de Guanta [sic; Huanta] en el valle de Coquimbo a una altura de 6 ó 7,000 pies" [1935–2260 m], Nov. 1836, *C. Gay s.n.* (holotype, P not seen; isotype, SGO).

Perennials, densely puberulous to villosulous throughout, from well-developed taproots to 5(10) mm thick, with red bark frequently peeling in plates; stems usually 5–10, to 15 cm long, weak. *Leaves* simple, subsessile; *blades* elliptic to narrowly so, 15–40 mm long, 4–7 mm wide, sharply acute at apex, acute to attenuate at base, subcoriaceous; *stipules* at more basal nodes deltoid to broadly triangular, 1.5–2 mm long, acute to shortly bifid or bilobed, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to ligulate, 2.5–4 mm long, acute to acuminate, erose. *Inflorescences* 1–4 cm long and wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to acuminate at apex, acute at base, central lobe 24–35 mm long, 3.5–10 mm wide, lateral lobes 2, 14–28 mm long, 2–4 mm wide; *flowers* with hypanthium ca. 1 mm long; *calyx* limb pilosulous, lobes (4)5, equal, elliptic to oblanceolate, 10–15 mm long, 2–5 mm wide, acute at apex and base, entire or erose with minute appendages; *corolla* externally moderately to densely pilosulous, tube 18–24 mm long, 0.4–0.8 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 2.5–3 mm diam., lobes (4)5, 4–5 mm long, 1–2 mm wide at base; *anthers* 2–2.5 mm long, filaments 1.5–2 mm long in short-styled form; *stigmas* 0.5–1 mm long, in long-styled form exserted by 2–3 mm. *Capsules* ca. 5 mm long and wide, persistent calyx lobes 12–23 mm long, 3–5 mm wide; *seeds* 2–3 mm long, 1–2 mm wide. Illustrations: Ricardi (1963a: fig. 4, as "*Oreopolus palma*"), Squeo et al. (1994: fig. 78, as "*Oreopolus palmae*").

Distribution and habitat. Andean Cordillera of central Chile (30°–33°30′S) at 2000–4000 m, in open sand or rubble. Collected in flower November through March, in fruit January through March.

This species is distinguished by its simple cauline leaves that are acute at the apex, and five calyx lobes that are all similar in form and size, elliptic to oblanceolate, and 10–15 mm long in flower becoming 12–23 mm long in fruit. It is similar vegetatively to *Cruckshanksia hymenodon,* which can be distinguished by its usually two or three petaloid calyx lobe appendages, and to *C. macrantha,* which can be distinguished by its leaves, which are 8–15 mm long and obtuse to rounded at the apex. The consistently trilobed inflorescence bracts were not included in Ricardi's (1963a) description of this species. The fruits are described for the first time here.

The specific epithet commemorates Señor Ga-

briel Palma, so although it was originally published as "*palma,*" it must be corrected to "*palmae.*" The name "Cruckshanksia virescens Clos" was written on labels of at least one of Gay's collections of this species, but was never published.

Representative specimens examined. CHILE. IV REGION. **Prov. Choapa**: 2 hrs. by horse E of Cuncumen, *Morrison 16999* (CONC, GH). **Prov. Elqui**: at dam, La Laguna, ca. 108 km from Rivadavia, *Johnston 16388* (GH, K, MO). **Prov. Limari**: Río Blanco, *Jiles 1124* (CONC, M). V REGION. **Prov. Cordillera**: in valle San Ramón, *Grandjot s.n.* (CONC–1074, CONC–55546, M, MO–1063540, MO–116091).

2. Cruckshanksia macrantha Phil., Linnaea 33: 97. 1864. *Oreopolus macranthus* (Phil.) Ricardi, Gayana, Bot. 6: 14. 1963. TYPE: Chile. IV Region. Prov. Coquimbo: Quebrada Escondida, 1860–1861, *Volckmann s.n.* (holotype, SGO–56866; isotype, CONC–43455).

Perennials, densely and finely puberulent to villosulous throughout, forming mats to 1 m or more diam., from well-developed taproots to 5(10) mm thick with red bark often peeling in large flakes; stems 3–30, to ca. 15 cm long, weak. *Leaves* simple, subsessile; *blades* narrowly to rather broadly elliptic to lanceolate, oblanceolate, or ligulate, 8–15 mm long, 2–5 mm wide, obtuse to rounded at apex, acute to rounded and then abruptly attenuate at base, subcoriaceous; *stipules* at more basal nodes broadly triangular, 0.8–1 mm long, acute to usually bilobed or shortly bifid, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to ligulate, 0.8–1 mm long, acute to rounded, erose. *Inflorescences* 1–2 cm long and wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to rounded at apex, acute to attenuate at base, central lobe 4–11 mm long, 1–5 mm wide, lateral lobes 2, 4–10 mm long, 1–2 mm wide; *flowers* with hypanthium 1.5–2[2.5] mm long; *calyx* limb densely pilosulous, lobes (4)5, equal, elliptic to oblanceolate, 3.5–5 mm long, 0.8–2 mm wide, acute at apex and base, entire or erose with appendages 0.5–1 mm long; *corolla* externally moderately to densely pilosulous, tube 18–23 mm long, 0.3–0.6 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 1.5–2 mm diam., lobes 5, 4–6 mm long, 1–2 mm wide at base; *anthers* 1.5–2 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 0.5–1[2] mm long, in long-styled form exserted by 1–3 mm. *Capsules* 3–5 mm long, 3.5–8 mm wide, persistent calyx lobes 7–17 mm long, 2.5–10 mm wide; *seeds* 2.5–3 mm long, 1.5–2 mm wide. Illustrations: Ricardi (1963a: fig. 5, as "*Oreopolus macranthus*"); Squeo et al. (1994: fig. 77, as "*Oreopolus macranthus*").

Distribution and habitat. Andean Cordillera of northern Chile and adjacent Argentina (26°30′–32°15′S) at 1100–4300 m, most frequently collected above 3000 m. Collected in flower November through February, in fruit January through February.

This species is distinguished by its simple cauline leaves that are obtuse to rounded at the apex, and by the five calyx lobes that are similar in form and size, elliptic to oblanceolate, and 3.5–5 mm long in flower becoming 7–15 mm long in fruit. It is similar to *Cruckshanksia lithiophila,* which can be distinguished by its calyx lobes all bearing petaloid appendages with slender stipes; these species may not be distinct (see discussion under that species). It is also similar to *C. palmae,* which can be distinguished by its leaves which are 15–40 mm long and acute at the apex. The consistently trilobed inflorescence bracts were illustrated for this species by Ricardi (1963a: fig. 5D) but not included in his description. The fruits are described for the first time here.

Representative specimens examined. ARGENTINA. **San Juan:** Junta del Río Cura, Río de la Tagua below its confluence with the Río de la Sal, *Johnston 6162* (CONC, F, GH). CHILE. III REGION. **Prov. Chañaral**: cerca del Salar de Pedernales, *Zöllner s.n./herb. Garaventa 5324* (CONC), *Zöllner 786* (CONC). **Prov. Copiapó**: Cordillera Río Turbio, Cerro Cadillal, *Werdermann 936* (CONC, E, F, GH, M, MO, NY). **Prov. Huasco**: Laguna Valeriano, *Johnston 6065* (CONC, F, GH, K). IV REGION. **Prov. Choapa**: Río Piuquenes, *San Román s.n.* (CONC–29868). **Prov. Elqui**: Baños del Toro, Doña Ana, *Werdermann 222* (CONC, E, F, GH, K, MO).

3. Cruckshanksia lithiophila Ricardi, Gayana, Bot. 7: 3. 1963. TYPE: Chile. III Region. Prov. Copiapó: Quebrada Vizcachas, a 43 km de La Puerta, 3100 m, 1 feb. 1963, *M. Ricardi, C. Marticorena & O. Matthei 659* (holotype, CONC–28752; isotype, SGO–73933).

Perennials, puberulent to densely villosulous throughout, from well-developed taproots to 2.5 cm thick with red corky bark; stems 10–30, to ca. 10 cm long, weak. *Leaves* simple, subsessile; *blades* lanceolate to elliptic, 5–20 mm long, 2–7 mm wide, obtuse at apex, attenuate at base, subcoriaceous; *stipules* at more basal nodes triangular, 1–2 mm long, acute to usually bilobed, erose, at more distal nodes deeply bilobed, lobes triangular, 1–6 mm long, acute, erose. *Inflorescences* 1–2.5 cm long and 1–4 cm wide excluding corollas; bracts with lobes narrowly elliptic to oblanceolate, acute to rounded

at apex and base, central lobe 9–21 mm long, 3–6 mm wide, lateral lobes 2, 9–18 mm long, 2–5 mm wide; *flowers* with hypanthium 1–1.5 mm long; *calyx* limb villosulous, lobes 5, equal, entire or erose with appendages 0.5–3 mm long, with stipes 3–6 mm long, appendages elliptic to ovate, 3–5 mm long, 2–4 mm wide, obtuse to rounded at apex, cuneate at base, somewhat petaloid, color unknown; *corolla* externally pilosulous, tube 10–14.5 mm long, 0.3–0.8 mm diam. near middle, enlarged throat of long-styled form 1.5–3 mm long and 1.5–2 mm diam., lobes 5, 2–3 mm long, 1–1.5 mm wide at base [Ricardi (1963b) said 2–2.5 mm long, but his illustration shows the lobes ca. 4 mm long if the proportions are correct]; *anthers* 1–1.5 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 1–1.5 mm long, in long-styled form exserted by 1–2 mm. *Capsules* 4–4.5 mm long, ca. 4 mm wide, persistent calyx lobes with stipes 10–15 mm long and appendages ovate, 9–13 mm long, 5–8 mm wide, acuminate; *seeds* 3–4 mm long, ca. 2 mm wide. Illustrations: Ricardi (1963b: figs. 1, 2); Ricardi and Quezada (1963: fig. 2).

Distribution and habitat. Andean Cordillera of northern Chile (27°–27°50′S) at 3300–3600 m, in open rubble. Collected in flower and fruit generally concurrently in November, January, and March.

This infrequently collected species is distinguished by its simple cauline leaves that are obtuse at the apex, and by the five calyx lobes that are each composed of a stipe and petaloid appendage. It is similar and probably closely related to *Cruckshanksia macrantha,* which is distinguished by its elliptic to oblanceolate calyx lobes that are narrowed but not stipitate at the base and generally shorter (3.5–5 mm long in flower and 7–17 mm long in fruit). These two species are maintained here, although considering the variability found in other species of *Cruckshanksia, C. lithiophila* may represent only a well-marked variant of *C. macrantha.* The difficulty of distinguishing these species is demonstrated by *Werdermann 936*: the specimens at F and NY were annotated by Ricardi as "*Oreopolus macranthus*" (i.e., *C. macrantha*), while the specimen at GH, which appears similar in all respects, was identified by him as *C. lithiophila.*

The petaloid calyx lobe appendages are usually not well developed at anthesis but enlarge markedly as the fruit develops. Ricardi's description (1963b) does not make this distinction; his measurements apply to the fruiting stage.

Additional specimens examined. CHILE. III REGION. **Prov. Copiapó**: quebrada Chinches, vega Chinches, *Marticorena et al. 537* (CONC); quebrada El Colorado, a mitad de falda, *Marticorena et al. 582* (CONC); quebrada de Vizcachas, *Ricardi & Marticorena 3779* (CONC); camino internacional de Copiapó a Tinogasta, quebrada Codocedo, *Villagrán & Arroyo 4668* (CONC).

4. Cruckshanksia hymenodon Hook. & Arn., Bot. Misc. 3: 361. 1833. TYPE: Chile. IV Region. Prov. Coquimbo: Coquimbo, *Cruckshanks 3* (lectotype, designated here, E). SYNTYPES: Chile. IV Region. Prov. Coquimbo: Coquimbo, *Cuming 861* (K), = *Cruckshanksia montiana*; *Cuming 875* (K), = *Cruckshanksia montiana.*

Rotheria lanceolata Meyen, Reise um die Erde 1: 402. 1843. TYPE: Unknown.

Cruckshanksia bustillosii Phil., Linnaea 28: 696. 1858. *Cruckshanksia hymenodon* var. *bustillosii* (Phil.) Ricardi, Gayana, Bot. 9: 16. 1963. TYPE: Chile. Region Metropolitana: Prov. Santiago: Cordillera de la prov. de Santiago, 1857, *Bustillos s.n.* (holotype, SGO–56889, photo GH).

Perennials, densely villous to pilosulous throughout, from well-developed taproots to 1(2) cm thick with corky reddened bark; stems 3–10, 15–30 cm long, weak. *Leaves* simple or rarely 2–3-lobed, petioles 1–3 mm long; *blades* elliptic to narrowly so or lanceolate, 7–30[40] mm long, 2–9.5[15] mm wide, acute at apex, attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes triangular, 2–4 mm long, acute to bilobed, entire to erose, at more distal nodes deeply bilobed, lobes triangular, 2–4 mm long, acute to acuminate, erose with appendages to 1 mm long. *Inflorescences* 1–3 cm long and 2–10 cm wide excluding corollas; bracts with lobes elliptic to narrowly so, acute at apex and base, central lobe 10–13 mm long, 3–7 mm wide, lateral lobes 2(4), 8–12 mm long, 1–5 mm wide; *flowers* with hypanthium 1–1.5 mm long; *calyx* limb pilosulous to glabrescent, lobes (4)5(6), erose with appendages 0.4–5 mm long, unequal, (1)2–3(4) lobes with stipes 2–9 mm long, appendages ovate to suborbicular or oblong, 3–11 mm long, 2.5–11 mm wide, rounded to truncate at apex and base, petaloid, pink or sometimes white (often drying yellow), remaining lobes subulate and 4–10 mm long or infrequently similar to lobes of bracts and 3–8 mm long by 1–2 mm wide; *corolla* externally moderately to densely pilosulous, tube 9–23[26] mm long, 0.3–1 mm diam. near middle, enlarged throat of long-styled form 1.5–3[4] mm long and 1.5–2 mm diam., lobes 5, 3–4 mm long, 1–2 mm wide at base; *anthers* 1.5–2[2.5] mm long, filaments 1–2 mm long in short-styled form; *stigmas* 1–2 mm long, in long-styled form exserted by 1–3 mm. *Capsules* 3–4 mm long, 3.5–4 mm wide, persistent calyx lobes with stipes 4–9 mm long and appendages 5–11 mm long, 4–

11 mm wide; *seeds* ca. 2 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: fig. 3), Schumann (1891: fig. 8Q, R).

Distribution and habitat. Northern Chile and adjacent Argentina (26°–33°50′W) in arid regions at 20–2950 m. Collected in flower and fruit usually concurrently, at low elevations in October and November, at high elevations December through March.

This is the most commonly collected species of *Cruckshanksia.* It is distinguished by its dense villous to pilosulous pubescence on all vegetative parts, usually simple cauline leaves, and calyx with usually 2–3 lobes bearing pink or white petaloid appendages. Label data often describe the color of either the petaloid calyx appendages (pink or white) or the corollas (yellow) without specifying which structure is described, and this has been the source of some confusion. Additionally, the pink petaloid appendages frequently become yellow when dried.

In the original description of *Cruckshanksia hymenodon,* Hooker and Arnott noted that two different forms could be distinguished, "α. foliis incanis" and "ß. foliis minus pubescentibus," and cited a collection made by Cruckshanks for the first and two collections by Cuming for the second. These two forms correspond to what are here considered two distinct species, *C. hymenodon* and *C. montiana,* respectively. Although all previous authors have interpreted these taxa in this way, no one previously has clearly selected a lectotype. This is done here. Even though both of Cuming's collections have several duplicates and are more widely distributed than the single Cruckshanks specimen, this last specimen is chosen here in order to fix the application of this name to the species to which it was applied by Clos (1848) and all subsequent authors.

Ricardi and Quezada (1963) recognized two varieties in this species: var. *hymenodon* and var. *bustillosii.* They distinguished variety *bustillosii* in their key based on its "linear-lanceolate leaves, sepals 2, corollas 16–20 mm long, and plants with a tendency to form lawns," in contrast to "leaves mostly oblong-lanceolate, sepals 2–3(5), and corollas 26–30 mm long" in variety *hymenodon* (Ricardi & Quezada, 1963; my translation from the Spanish; no habit information given by them for var. *hymenodon*). They distinguished variety *bustillosii* in their diagnosis and discussion only by its "chamaephytic habit, linear-lanceolate leaves, and emarginate apex of the sepals" (Ricardi & Quezada, 1963; my translation from the Spanish; in their usage, "sepal" denotes only calyx lobes that bear petaloid appendages). However, many specimens bear some characteristics of both varieties and cannot be classified according to these criteria, including specimens studied by Ricardi and Quezada. For example, *Werdermann 158,* placed by them in variety *hymenodon,* has corollas 18 mm long and petaloid calyx lobe appendages that vary from obtusely angled to truncate or in a few flowers shortly emarginate, and *Wagenknecht 18505* (CONC, GH, MO), also placed by them in variety *hymenodon,* has several petaloid calyx lobe appendages that are as deeply emarginate as those shown in their illustration of variety *bustillosii,* along with others that are obtusely angled. Several leaves on specimens identified as variety *bustillosii* (e.g., *Worth & Morrison 16568*; *Morrison 16998*) are similar in shape to those of typical variety *hymenodon,* although they are generally shorter than the average (but not the extreme) for variety *hymenodon* and some other leaves on the same plant are relatively narrower. The plants segregated as variety *bustillosii* are all from relatively higher elevations, but specimens of variety *hymenodon* are cited from throughout this same range, so no geographic or ecological difference is evident. The plants classified as variety *bustillosii* are generally markedly smaller in stature, and on collections with abundance indicated they are usually said to be rare or infrequent, in contrast to the usual description of the larger, more robust plants of variety *hymenodon* as common or abundant. It seems likely that these plants are no more than reduced representatives of this species, probably due to microhabitat conditions, and this variety is not recognized here.

Representative specimens examined. ARGENTINA. **San Juan:** Departamento Calingasta, al S de Barreal, Mantiales, *Kiesling et al. 8051* (MO, SI). CHILE. III REGION. **Prov. Chañaral**: 19 km al interior de Llanta, *Ricardi et al. 1563* (CONC). **Prov. Copiapó**: ca. 40 km S of Copiapó along Rte. 5, ca. 2 km N of the entrance to Mina Flor del Llano, *Taylor et al. 10781* (CONC, MO), *10782* (CONC, MO). **Prov. Huasco**: Alto del Carmen, *Werdermann 158* (E, GH, K, M, MO). IV REGION. **Prov. Choapa**: La Vega Escondida, 3 hr. by horse E of Cumcumen, *Morrison 16998* (GH, MO). **Prov. Elqui**: Baños del Toro, *Werdermann 211* (E, F, GH, K, M, MO), *Zöllner 10392* (MO). **Prov. Limari**: Los Molles, *Jiles 4762* (CONC, M). V REGION. **Prov. Petorca**: Cerro Chache, 5 hr. by horse SE of Patagua Mine, 18 km E of La Ligua, *Morrison 17025* (GH, MO). REGION METROPOLITANA. **Prov. Cordillera**: Lagunillas, *Zöllner 10644* (MO).

5. Cruckshanksia pumila Clos, in Gay, Fl. Chil. 3: 196. 1848. TYPE: Chile. IV Region. Prov. Coquimbo: "vecindad de Arqueros, 8bri 1836," *C. Gay 242* [holotype, P not seen, photo (neg. #4646) SGO; isotypes, P not seen, photo (neg. #4647) SGO, probable isotype F–972004].

Cruckshanksia tripartita Phil., Viage Des. Atacama 200. 1860. TYPE: Chile. III Region. Prov. Chañaral: Pan de Azucar, *R. A. Philippi s.n.* (holotype, SGO–56883; isotype, SGO–43336/herb. F. Philippi 951).

Cruckshanksia chrysantha Phil., Anales Univ. Chile 41: 730. 1872. TYPE: Chile. III Region. Prov. Huasco: Yerbas Buenas, Oct. 1871, *T. King s.n.* (holotype, SGO–56904; isotypes, E, GH, K-ex herb. E. C. Reed, photo (neg. #2472) SGO, SGO–43356/herb. F. Phil. 948b, SGO–43348/herb. F. Phil. 948a, photo GH).

Cruckshanksia geisseana Phil., Anales Univ. Chile 85: 737. 1894. TYPE: Chile. III Region. Prov. Copiapó: Cerro Bandurrias, 1885, *W. Geisse s.n.* (lectotype, designated here, SGO–43365/herb. F. Phil. 1935, photo SGO; isotype, GH).

Cruckshanksia darapskyana Phil., Anales Univ. Chile 85: 738. 1894. TYPE: Chile. II Region. Prov. Antofagasta: Taltal, 1889, *Dr. L. Darapsky s.n.* (holotype, SGO–56884; isotype, SGO–43346/herb. F. Phil. 2318, photo GH).

Annuals or rarely apparently perennials, puberulent to densely villosulous or pilosulous throughout (above hypocotyl), from a solitary short to well-developed taproot 1–2.5 mm thick with smooth gray or brown epidermis; stems to ca. 15 cm long, usually 1–4 times branched but occasionally more or not at all, ascending to weak; *cotyledons* sessile, narrowly oblanceolate to ligulate, 8–16 mm long, 1.5–3 mm wide, at apex truncate to rounded, at base attenuate, fleshy drying coriaceous, glabrous, with stipules interpetiolar, fused to bases of cotyledons, membranaceous, interpetiolar portion truncate to broadly triangular, 1–2 mm long, entire to shortly bifid or erose. *Leaves* simple or rarely 2-lobed, petioles (0.5)2–7 mm long; *blades* elliptic to usually narrowly so or oblanceolate, (4)12–30 [40] mm long, (2)3–8 mm wide, acute at apex, acute to usually attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes deeply bilobed, lobes triangular to narrowly so, 1–4 mm long, acute to acuminate, erose with appendages to ca. 1 mm long, at more distal nodes similar or more deeply lobed to completely divided. *Inflorescences* 1–2.5 cm long and 1–6 cm wide excluding corollas; bracts with lobes elliptic to narrowly so, acute at apex and base, central lobe 8–34 mm long, 3–4 mm wide, lateral lobes 2(4), 5–15 mm long, 2–4 mm wide; *flowers* with hypanthium 0.5–1.5 mm long; *calyx* limb pilosulous, lobes 4–5, erose with appendages 1–4 mm long, unequal, (0)1–2 lobes with stipes 2–7 mm long, appendages elliptic to suborbicular, 2–10 mm long, 5–10 mm wide, obtusely angled to rounded or subtruncate and usually mucronate at apex with mucro 0.5–1 mm long, rounded to truncate or somewhat cordate at base, petaloid, bright to deep yellow, remaining lobes subulate, 2.5–8 mm long; *corolla* externally moderately to densely pilosulous, tube 9–12 mm long, 0.1–0.3 mm diam. near middle, enlarged throat of long-styled form 1–1.5 mm long and diam., lobes 5, 1–2.5 mm long, 0.5–1 mm wide near base; *anthers* 1–1.3 mm long, filaments 1–1.5 mm long in short-styled form; *stigmas* 1–2 mm long, in long-styled form exserted by 1–1.5 mm. *Capsules* 2–3 mm long, 2–3.5 mm wide, persistent calyx lobe appendages to 13 mm long, 15 mm wide; *seeds* ca. 1.5 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: Fig. 5, as "*C. tripartita,*" and Fig. 9 but in Fig. 9A the stipules at more distal nodes are not entirely accurate and Fig. 9B shows a stipule of a relatively basal node).

Distribution and habitat. Northern Chile (23° 30′–30°10′S) at 10–1900 m, in arid regions. Collected in flower and fruit concurrently, September through December.

This frequently collected species is distinguished by its annual habit, usually simple cauline leaves, calyx with usually 1–2 lobes prolonged into yellow petaloid appendages, and relatively small flowers with slender tubes.

Ricardi and Quezada (1963) separated *Cruckshanksia tripartita* from *C. pumila,* commenting that Johnston (1929) had combined them but the taxa seemed distinct. Philippi in his original description separated *C. tripartita* based on its larger, more branched inflorescence, but this feature intergrades continuously with plants he placed in *C. pumila* and appears to represent only an advanced developmental stage. Ricardi and Quezada commented in their discussion under *C. tripartita* that these species are separated by their "habit, pubescence, stipules, and floral characteristics" (my translation from the Spanish), but in their key to species they separated these only by the stipules "non-interpetiolar, setaceous, entire, to 4 mm long" in *C. tripartita* in contrast to "interpetiolar, triangular-long acuminate, laciniate-ciliate, to 2 mm long" in *C. pumila.* As discussed in the morphology section (above), these stipule forms represent developmental stages that may be found on the same stem, and both conditions are found on most specimens cited for each of these species by Ricardi and Quezada. This stipule distinction thus serves primarily to separate plants that flower precociously from those that show more vegetative development. When the distinctions in this key are applied, the individual plants of one population are sorted into two species (e.g., *Taylor 10764,* CONC, MO; *10793,* CONC, MO). No pattern is evident in any other features, and *C. tripartita* is here combined with *C. pumila.*

Ricardi and Quezada (1963) cited "Huanta, 'in

collibus arenosis, 8bri 1836', leg. *C. Gay* (SGO)," as the "isotype" of *Cruckshanksia pumila*. These data correspond to two specimens, CONC–28802 and SGO–56885, which additionally both bear the collection number *1929*. However, this information does not agree with the locality cited in the original species description, "en los arenales porfíricos de la vecindad de Arqueros," so these specimens apparently are not types. Ricardi and Quezada (1963) listed several Geisse collections made in 1885 and 1886 and deposited at SGO as "types" and one at GH as an "isotype" of *C. geisseana*. Philippi gave the type locality for this species as "prope Bandurrias haud procul a Chañarcillo detexit orn. Gulielmus Geisse," and judging from annotations at SGO most likely based his description on most or all of the set of specimens sent to him by William Geisse with collection dates of 1886 or earlier. These specimens are here considered syntypes. From them, the one best represented in several herbaria is chosen here as the lectotype. These collections have been variously attributed to "W. Geisse," "Guill. Geisse," "Guillermo Geisse," and "G. Geisse."

Many of the "perennial" specimens cited by Ricardi and Quezada (1963) represent annual plants with well-developed taproots, or have here been referred to *Cruckshanksia hymenodon*. The few apparently truly perennial specimens of *C. pumila* (*Jaffuel 2628*, CONC, GH; *Jiles 5370*, CONC; *Ricardi & Parra 77*, CONC) are additionally characterized by relatively small leaves and petaloid calyx appendages, although these all fall within the range of sizes found among the annual plants. These plants are all from the Taltal area, and may represent a distinct population. Only the apparently perennial habit distinguishes them, however, and they are here provisionally included in *C. pumila*.

Representative specimens examined. CHILE. II REGION. **Prov. Antofagasta**: Taltal, near Paposo, Cerro Yumbes, *Johnston 5560* (CONC). III REGION. **Prov. Chañaral**: Carretera Panamericana, entre Las Bombas y Chañaral, Km 27, *Ricardi et al 1430* (CONC). **Prov. Huasco**: Rte. 5 between Domeyko and Vallenar, ca. 20 km N of Domeyko, *Taylor et al. 10679* (CONC, MO). **Prov. Copiapó**: entre Vallenar y Copiapó, a 39 km de Copiapó, *Ricardi et al. 663* (CONC). IV REGION. **Prov. Elqui**: Rivadavia, *Montero 11687* (CONC), *Ricardi 2178* (CONC). **Prov. Limari**: Corral Quemado, *Jiles 3484* (CONC).

6. Cruckshanksia montiana Clos, in Gay, Fl. Chil. 3: 195. 1848. TYPE: Chile. IV Region. Prov. Coquimbo: "dunas cerca de La Serena, 7bri 1836," *C. Gay 1931* (holotype, P not seen; isotypes, CONC–43456, GH, K, NY, SGO–56880, and possibly F–635148).

Cruckshanksia capitata Philippi, Anal. Univ. Chile 41: 731. 1872. TYPE: Chile. III Region. Prov. Huasco: Carrizal Bajo, *T. King s.n.* (holotype, SGO–56879; isotype, SGO–43367/herb. F. Phil. 944, photo GH).

Cruckshanksia densifolia Philippi, Anal. Univ. Chile 41: 730. 1872. *Cruckshanksia capitata* var. *densifolia* (Philippi) Reiche, Anal. Univ. Chile 106: 973. 1900. TYPE: Chile. III Region. Prov. Huasco: Carrizal Bajo, 1871, *T. King s.n.* (holotype, SGO–56882, photo GH; isotype, E).

Perennials, puberulent to densely villosulous throughout, from well-developed taproots 1.5 cm thick with red corky bark; stems 5–15, to ca. 20 cm long, weak. *Leaves* simple with petioles 1–5 mm long or sometimes 3-lobed and sessile; *blades* narrowly elliptic, 8–23 mm long, 0.8–4(6) mm wide, acute and sometimes mucronate at apex with mucro to ca. 0.5 mm long, attenuate at base, membranaceous to subcoriaceous; *stipules* at more basal nodes triangular, 1–3 mm long, acute to shortly bilobed, entire to slightly erose, at more distal nodes deeply bilobed, lobes triangular to narrowly so, 1.5–7 mm long, acute, erose with appendages to ca. 1 mm long. *Inflorescences* 1–3.5 cm long and 2–4.5 cm wide excluding corollas; bracts with lobes narrowly elliptic to narrowly oblanceolate, acute at base and apex, central lobe 10–17 mm long, 1.5–4 mm wide, lateral lobes 2–4, 8–15 mm long, 1–2.5 mm wide; *flowers* with hypanthium 1.5–2 mm long; *calyx* limb pilosulous, lobes (4)5(6), erose with linear appendages 0.5–4 mm long, unequal, (1)2–3(4) lobes with stipes 6–10 mm long, appendages orbicular to oblong or somewhat reniform, 6–10 mm long, 8–15 mm wide, rounded to usually truncate and mucronate at apex with mucro 0.5–1 mm long, rounded to truncate at base, petaloid, bright to deep yellow, remaining lobes subulate and 4–10 mm long or occasionally similar to bracts, 3–8 mm long, 0.5–1.5 mm wide; *corolla* externally moderately to densely pilosulous, tube 10–13 mm long, 0.3–0.6 mm diam. near middle, enlarged throat of long-styled form 1–1.5[3] mm long and diam., lobes 5, 2–4.5 mm long, 1–2 mm wide at base; *anthers* 1–1.5[2] mm long, filaments ca. 1–2 mm long in short-styled form; *stigmas* ca. 1 mm long, in long-styled form exserted by 1–2 mm. *Capsules* 2.5–3[4] mm long, ca. 3[4] mm wide, persistent calyx lobe appendages to 12 mm long, 18 mm wide; *seeds* 1.5–2 mm long, ca. 1 mm wide. Illustrations: Ricardi and Quezada (1963: fig. 6, fig. 7, as "*C. capitata*").

Distribution and habitat. Northern Chile, in arid regions at 10–500 m. Collected in flower and fruit usually concurrently, September through November.

This species is distinguished by its usually simple narrow cauline leaves with the secondary ve-

nation not evident and calyx with usually 2–3 lobes prolonged into yellow petaloid appendages. It is similar to *Cruckshanksia verticillata,* as discussed under that species.

Ricardi and Quezada (1963) separated *Cruckshanksia capitata* based on the form of the stipules and petaloid calyx lobe appendages. However, as discussed in the morphology section (above), both of these features vary with developmental stage, usually along a single stem. The stipule form by which they distinguished "*C. capitata*" is that characteristic of more basal nodes and the form of the petaloid calyx lobe appendages they used is that found on the flowers, while the forms by which they distinguished "*C. montiana*" are those of the most distal nodes and the fruiting stage, respectively. Most of the specimens they cite show both of the conditions they used to separate these species, and consequently *C. capitata* is here combined with *C. montiana.*

Cruckshanksia montiana was named in honor of Señor Manuel Montt, but originally published with the spelling "*montiana.*" This epithet has been improperly corrected by various authors to "*monttiana,*" and has also been misspelled as "*montteana*" and "*montana.*" As discussed in detail under the treatment of *Cruckshanksia hymenodon,* Hooker and Arnott originally based their description of that species on three specimens, two of which represent *C. montiana.*

Representative specimens examined. CHILE. III REGION. **Prov. Copiapó**: Quebrada del León, *Billiet & Jadin 5356* (BR, MO), *Werdermann 434* (CONC, E, GH, K, M, MO). **Prov. Huasco**: Huasco, *Werdermann 133* (CONC, E, GH, K, MO). IV REGION. **Prov. Elqui**: road from La Serena to Punta Teatinos, *West 3918* (CONC, GH, MO).

7. Cruckshanksia verticillata Phil., Anal. Univ. Chile 85: 737. 1894. TYPE: Chile. II Region. Prov. Antofagasta: Bandurrias, 1886, *W. Geisse s.n.* (holotype, SGO–56873/herb. F. Phil. 1936; isotype, SGO–56878, photo GH).

Cruckshanksia paradoxa Phil., Anal. Univ. Chile 85: 738. 1894. *Cruckshanksia capitata* var. *paradoxa* (Phil.) Reiche, Anal. Univ. Chile 106: 973. 1900. TYPE: Chile. II Region. Prov. Antofagasta: Pajonales, Nov. 1887, *W. Geisse s.n.* (lectotype, designated here, SGO–72374).

Perennials, puberulent to villosulous or pilosulous throughout, from well-developed taproots to 6 mm thick with somewhat corky reddened bark; stems 2–10, to 10 cm long, weak. *Leaves* simple to usually 2–3-lobed, subsessile to sessile; *blades* narrowly to very narrowly oblanceolate, 7–18 mm long, 1–2 mm wide, acute and frequently falcate at apex, attenuate at base, membranaceous to subcoriaceous; *stipules* usually none or with 1 or 2 lobes, these separate, triangular, 1–1.5 mm long, 0.8–1 mm wide, acute to rounded, erose with appendages to ca. 1 mm long. *Inflorescences* 1–2 cm long and 1–3 cm wide including corollas; bracts similar to cauline leaves of most distal nodes; *flowers* with hypanthium 0.5–1 mm long; *calyx* limb villous to pilosulous, lobes 2, erose with linear appendages 0.5–3 mm long, equal, with stipes 4–6 mm long, appendages elliptic-oblong to suborbicular, 3–6 mm long, 2–7 mm wide, rounded and frequently mucronate at apex with mucro ca. 0.5 mm long, acute to cuneate at base, petaloid, yellow; *corolla* externally moderately to densely pilosulous, tube 12–14 mm long, 0.3–0.5 mm diam. near middle, enlarged throat of long-styled form 2–3 mm long and 1.5–2 mm diam., lobes 5, 3–3.5 mm long, 1–1.5 mm wide near base; *anthers* 1–1.3[2] mm long, filaments ca. 1 mm long in short-styled form; *stigmas* ca. 0.5 mm long, in long-styled form exserted by 1–2 mm. *Capsules* ca. 3 mm long and wide, persistent calyx lobe appendages enlarging slightly at most; *seeds* ca. 1.5 mm long, ca. 1 mm wide. Illustration: Ricardi and Quezada (1963: fig. 8).

Distribution and habitat. Northern Chile, in open sand and rubble of arid regions near Taltal at 100–1000 m. Collected in flower and fruit October through November.

This infrequently collected species is distinguished by its cauline leaves with usually two or three narrow lobes, and by the calyx limb reduced to two lobes, both with petaloid appendages. The cauline leaves are generally indistinguishable from the inflorescence bracts. It is similar and probably closely related to *Cruckshanksia montiana,* which can be distinguished by its usually simple cauline leaves and petaloid calyx lobe appendages 7–15 mm wide. Most features of *C. verticillata* are consistently smaller than those of *C. montiana* except the corollas, which are usually slightly longer, although these measurements overlap. These two species are maintained here, although considering the variability found in other species of *Cruckshanksia, C. verticillata* may represent only a well-marked variant of *C. montiana.*

The designation of type specimens for *Cruckshanksia verticillata* here follows annotations by Ricardi (in herb.) and citations in Ricardi and Quezada (1963). The lectotype chosen here for *C. paradoxa* is the only one of the syntypes that does not have some confusion attached to the label data.

Additional specimens examined. CHILE. III REGION. **Prov. Copiapó**: Bandurrias, 1885, *W. Geisse s.n.* [SGO–43368/herb. F. Phil. 1918, photo GH], 1885–1886, *W. Geisse s.n.* (GH, SGO–56875); Atacama, *com. Phil. 2/1888* [K not seen photo (neg. #SGO-2478) SGO]. IV REGION. **Prov. Elqui**: Pajonales, Nov. 1886, *W. Geisse s.n.* (SGO–72661).

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Appendix I. Index to numbered collections examined.

Identifications are indicated by numbers in parentheses following the collection number, as below. Asterisks indicate a type collection.

1 = *Oreopolus glacialis* (Poepp.) Ricardi
2 = *Cruckshanksia hymenodon* Hook. & Arn.
3 = *C. lithiophila* Ricardi
4 = *C. macrantha* Phil.
5 = *C. montiana* Clos
6 = *C. palmae* Clos
7 = *C. pumila* Clos
8 = *C. verticillata* Phil.

Arroyo, M. K. 81002 (4), 81042 (4), 81096 (4), 81112B (6), 81227 (2), 81619 (4), 81634 (4), 81681 (2), 83370 (2), 83403 (2), 83464 (4), 84555 (4), 83624 (2), 841003 (1), 850831 (1). Arroyo, S. C. 150 (1), 225 (1), 321 (1), 2243 (1), 2376 (1), 2513 (1), 3339 (1).

Bayern 352 (7). Betfruend 12438 (1). Billiet 5356 (5), 5570 (2). Boelcke 1694 (1), 3382 (1), 3410 (1), 3411 (1), 3546 (1), 5936 (1), 7228 (1), 10049 (1), 11114 (1), 11300 (1), 11669 (1), 13797 (1), 15106 (1), 15837 (1). Bridges 1207 (1), 1283 (1), 1299 (5), 1300 (5), 1301 (7), 1302 (2). Buchtien 1357 (1).

Cabrera 12624 (7). Castellanos 7908 (1). Cei 24176 (1). Comber 263 (1), 841 (1). Cordini 210 (1). Correa 2645 (1), 3059 (1), 3443 (1), 3566 (1), 3796 (1), 6346 (1), 8943 (1), 9091 (1), 9241 (1), 9992 (1), 10056 (1), 10237 (1), 10390 (1), 10442 (1). Covetto 7140 (1). Crespo 1645 (1), 2104 (1), 2287 (1). Cuming 861 (5), 875 (5), 1301 (7), 1302 (2).

Dawson 2624 (1). Diem 3224 (1). Donat 77 (1), 172 (1), 177 (1), 364 (1).

Elliot 22 (7). Eskuche 1121 (1).

Flores 25 (7). Furlong 40 (1).

Garaventa 4231 (7), 4400 (7), 4732 (2). Gardner 4535 (1). Gay 133 (5), 412 (2), 413 (6), 865 (5), 1255 (1). Gerling 5756 (1). Gigoux 217 (7), 220 (8), 627 (2). Gliesner 29 (7). Goodall 14 (1), 3955 (1), 4283 (1), 4380 (1). Grau 2043 (7), 2109 (7), 2118 (7), 2522 (2), 2540 (7), 2897 (1). Greninger 14 (2).

Hoffman 43 (7). Hosseus 245 (1), 601 (1), 1324 (1), 1332 (1). Hunziker 4845 (4), 7086 (1).

Illin 43 (1), 55 (1), 138 (1), 456 (1), 5524 (1), 5526 (1), 5736 (1), 5762 (1), 18146 (1).

Jaffuel 1158 (7), 2628 (7). Jiles 1124 (6), 1167 (2), 1199 (6), 1301 (7), 1571 (2), 2194 (7), 2225 (7), 2417 (2), 2427 (7), 2486 (6), 2571 (2), 2965 (6), 3147 (7), 3309 (2), 3484 (7), 3687 (7), 3758 (6), 3803 (2), 3917 (2), 3942 (7), 3992 (7), 4079 (2), 4167 (6), 4273 (2), 4762 (2), 4983 (5), 5064 (4), 5107A (2), 5273 (2), 5370 (7), 5442 (7), 5508 (2), 5803 (7), 5812 (2), 6354E (5), 6396 (2), 6505 (4). Johnston 3671 (2), 4784 (7), 4818 (2), 4872 (2), 4910 (2), 4974 (2), 5106 (7), 5160 (7), 5301 (7), 5560 (7), 5595 (7), 5711 (7), 5930 (4), 6065 (4), 6162 (4).

Kausel 3747 (7). Kiesling 8051 (2). King 26 (7), 51 (2). Krapov 4128 (1), 4288 (1). Krapovickas 5698 (4), 5726 (2). Kurtz 9570 (2). Koslowsky 115 (1), 5528 (1).

Landero 630 (1). Lechler 2895* (1). Leuenberger 3403 (1). Lobb 435 (5), 436 (7).

Magens 62 (1). Marticorena 1 (2), 63 (1), 207 (2), 244 (7), 248 (7), 328 (7), 495 (2), 537 (3), 582(3), 1030 (1), 1264 (7), 1387 (1), 1656 (7), 1678 (2), 1684 (2), 1699 (7), 9810 (2). Merxmüller 24996 (1). Meyer 9637 (1). Molina M. 34 (1). Montero 11687 (7). Moore 2264 (1). Morong 54 (2), 55 (7), 107 (8), 1106 (2), 1109 (2), 1303 (5). Morrison 16963 (2), 16998 (2), 16999 (6), 17025 (2), 17443 (2). Muniez 159 (1). Muñoz 2726 (2), 2837 (7), 2955 (7).

O'Donell 3748 (1).

Pereyra 2166 (1), 5306 (1). Pérez 23404 (2). Peterson 270.33 (1). Pirion 79 (1), 126 (1). Pisano 3660 (1), 4174 (1), 4730 (1), 4781 (1), 5604 (1). Poeppig 59* (1).

Rechinger 63338 (7), 63339 (2), 63476 (7), 63494 (7). Ricardi 12 (2), 77 (7), 378 (1), 484 (1), 515 (1), 533 (2), 552 (2), 663 (7), 980 (1), 1102 (2), 1131 (2), 1136 (5), 1250 (7), 1430 (7), 1462 (2), 1489 (2), 1563 (2), 1569 (2), 1718 (2), 1740 (6), 1750 (6), 1783 (4), 1788 (4), 2178 (7), 2232 (2), 2275 (7), 2351 (1), 2459 (7), 2524 (7), 2528 (2), 2586 (7), 2627 (7), 2634 (7), 3051 (7), 3139 (7), 3766 (2), 3779 (3), 3970 (5), 4359 (7), 5074 (1), 5139 (1), 5527 (7), 5663 (1). Rodraguéz 10 (2), 77 (5). Rodriguez 40 (2), 1616 (7). Roig 11973 (2), 13019 (2), 13032 (2), 13043 (2). Romanczuk 954 (1). Rosas 1012 (7), 1169 (2), 1248 (2), 1256 (5), 1844 (1). Rose 19338 (7). Rossow 1310 (1), 1325 (1), 1463 (1), 1872 (1), 1617 (1), 1651 (1), 2662 (1), 4565 (1). Ruiz l. 3131 (1), 7175 (1), 11689 (1), 11727 (1), 15678 (1), 15736 (1), 16833 (1), 21441 (1).

Sánchez 293 (1), 442 (1), 552 (1). Santesson 1272 (1).

Schlegel 937 (6), 2415 (6), 5716 (5), 5886 (2). Seibert 300 (1). Semper 13992 (2). Senn 4269 (1). Silvestri 5744 (1). Solbrig 3040 (5), 3067 (7). Soriano 2026 (1), 2459 (1), 3067 (1). Sparre 10936 (1). Spegazzini 52 (1), 158 (1), 207 (1), 339 (1). Squeo 88008 (4), 88055 (4), 88082 (4), 88097 (4). Stuchart 18146 (1). Stuessy 11092 (1).

Taylor 10679 (7), 10764 (7), 10781 (2), 10782 (2), 10793 (7). TBPA 455 (1), 539 (1), 740 (1), 1669 (1), 2174 (1), 2330 (1), 2717 (1), 2854 (1), 3619 (1), 3758 (1). Teillier 557 (7), 657 (7), 731 (7), 968-969 [sic] (2).

Vervoorst 5626 (1). Villagrán 4668 (3). Volckmann 64 (2).

Wagenknecht 18120 (2), 18484 (7), 18505 (2), 18553 (7). Werdermann 112 (7), 133 (5), 158 (2), 211 (2), 222 (4), 434 (5), 810 (7), 936 (4). West 3918 (5), 4778 (1). Witte 35 (1). Worth 15835 (7), 16196 (2), 16233 (5), 16270 (2), 16388 (6), 16398 (2), 16565 (6), 16568 (2), 16682 (2).

Zöllner 787 (2), 786 (4), 5324 (4), 6015 (7), 6168 (7), 6196 (7), 6503 (7), 8455 (1), 8720 (7), 9312 (7), 9696 (1), 10002 (2), 10392 (2), 10644 (2), 10928 (5), 11376 (7), 14049 (2), 14819 (2), 18646 (7), 18693 (7), 18906 (2), 19124 (7), 19136 (7), 19138 (2).

A SURVEY OF THE REPRODUCTIVE BIOLOGY OF THE MYRTOIDEAE (MYRTACEAE)[1]

E. Nic Lughadha[2] *and C. Proença*[3]

ABSTRACT

The Myrtoideae usually present small, epigynous, 4–5-merous, polystemonous flowers that last one day. Bee-pollination in which pollen is the sole reward is the dominant pollination system. Nectar has been best documented in *Syzygium* but probably also occurs in other bee-pollinated genera. The most common bee visitors are Apidae: Meliponinae and Bombinae. Bird- and mammal-pollination occur in Old World *Syzygium* with nectar as the primary reward. Bird-pollination with petals as the reward occurs in New World *Acca* and *Myrrhinium*. General floral morphology is very uniform, while inflorescence types and flowering strategies are very diverse. Stigmas are dry and ovules are anatropous, hemicampylotropous or anacampylotropous and have an outer 2–6-layered integument and an inner 2-layered integument or a single integument. The ovary usually contains more ovules than will form seeds. Flowering strategies vary from mass-flowering types, in which the flowering episode typically takes only a few days, to steady-state types of up to 90 days duration. Flowering at dry/wet season transition is common in seasonal climates, and fire-induced flowering is found occasionally. Outbreeding is probably widespread, although both self-compatible and self-incompatible species exist. The self-incompatible species have self pollen tubes penetrating the micropyles, so preferential outcrossing may be maintained by a late-acting mechanism. Cryptic dioecy, in which female flowers have "mimic" sterile anthers occurs in several genera. Apomixis occurs in *Syzygium* and this has been reported to be linked to the polyembryony found in this genus. Myrtoid fruits are fleshy berries or drupes, dispersed by birds, bats, and other small mammals. Fruit size, color, texture, and number of seeds are all very variable. Seed coats may be absent to bony, but have a smooth surface. The endosperm is mainly digested by the developing embryo. Early embryology is relatively uniform but final embryo morphology varies widely across the genera. Germination times vary from 10 days to over 2 years and seed viability periods from 15 days to 1 year.

The reproductive biology of the Australian Myrtaceae has recently been the subject of a thorough review by Beardsell et al. (1993). The alliances traditionally assigned to the subfamily Leptospermoideae are the major focus of their account, reflecting not only the predominance of these groups in the Australian flora but also the widely acknowledged dearth of information on the reproductive biology of the Myrtoideae in general (e.g., van Wyk & Lowrey, 1988; Proença & Gibbs, 1994).

The present survey was compiled to complement that of Beardsell et al. (1993) by bringing together the scattered and often fragmentary data on the Myrtoideae. We use the term Myrtoideae in the traditional sense to embrace virtually all the fleshy fruited Myrtaceae. Thus we include Johnson and Briggs's (1984) monophyletic Myrtoideae sensu stricto, and their *Acmena* alliance (including *Syzygium*), although phylogenetic analysis has suggested that this latter group is more closely related to the leptospermoid *Eucalyptus* alliance than to the Myrtoideae s. str. (Johnson & Briggs, 1984). Conversely, we use the term Leptospermoideae in its broadest sense to include all Myrtaceae with capsular fruit. Where names have been changed to fit modern taxonomic concepts, the name that appeared in the original publication is cited in parentheses, e.g., *Syzygium paniculatum* (as *Eugenia paniculata*).

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The pantropical Myrtoideae as a whole has not received any synthetic taxonomic treatment since Niedenzu's (1893) synoptic account. There is no Old World equivalent to McVaugh's (1968) invaluable review of the American Myrtoideae. As a subfamily the Myrtoideae are rather less morphologically diverse than the Leptospermoideae. Approximately 60 genera are recognized for the estimated 2375 species of Myrtoideae, while the Leptospermoideae with less than half the number of species (1300) includes some 72 genera (species numbers from Schmid, 1980; generic estimates reflect the present authors' view of current taxonomic opinions). While this discrepancy may be interpreted as an artifact of our ignorance of the former group, most myrtologists would agree that the perceived homogeneity is real and has contributed to, rather than resulted from, the comparative taxonomic neglect which this subfamily has indisputably suffered. McVaugh (1968) described the species of American Myrtaceae as "distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter."

This homogeneity is portrayed in more concrete terms in Schmid's (1980) table of the "distinguishing organographic characters of the subfamilies of the Myrtaceae," the majority of which are based on reproductive organs. For each character a statement of the prevailing state within each subfamily is followed by a summary of the exceptions. Schmid expressed the estimated percentage of exceptions using precise and clearly defined qualifying terms: "very rarely" (signified < 2% of species), "rarely" (2–4%), "very occasionally" (5–10%), "occasionally" (5–30%) and "often" (31–60%). Hence a reasonably accurate impression of the variability of particular characters within the subfamilies can be gained. The qualifier "very rarely" is applied to the majority of the exceptions listed for the Myrtoideae. In the Leptospermoideae, however, exceptions are more or less evenly distributed across the range from "rarely" to "often" with "very rarely" being applied in only two instances. Thus the Myrtoideae emerges as a much more homogeneous group than the Leptospermoideae.

Inflorescence Structure

Inflorescences may be apical, subapical, axillary, supra-axillary, ramiflorous or cauliflorous in position. The authoritative analysis of inflorescence structure in the Myrtaceae by Briggs and Johnson (1979) documented an equally impressive range of structural form within the Myrtoideae. They range from many-flowered panicles and thyrsoids through dichasia, botryoids, metabotryoids, triads, and metaxytriads to monads and metaxymonads. In their brief description of adaptive syndromes, these authors drew attention to correlations between habitat, niche, and inflorescence arrangement. In particular, large panicles or aggregations of smaller inflorescences are reported by them as typical of forest and woodland species of Myrtaceae (myrtoid examples include species of *Myrcia* and its allies, *Blepharocalyx* (as *Temu*), *Pimenta, Xanthomyrtus,* species of *Syzygium* and its allies). However, in the undergrowth or understory of non-sclerophyllous communities, they noted that flowers are often in monads and/or triads that are not massed (myrtoid examples include *Myrceugenia, Psidium* spp., *Ugni, Myrteola, Myrtus* sensu stricto, *Rhodamnia, Lophomyrtus, Neomyrtus, Campomanesia, Luma,* and *Eugenia* spp.) (Briggs & Johnson, 1979). Ramiflorous or cauliflorous inflorescences have been linked to bat pollination (Crome & Irvine, 1986), and to bat or marsupial dispersal (see Fruit Characteristics and Dispersal Agents).

Flower Structure

Flowers of the Myrtoideae are hermaphrodite (or very rarely unisexual), epigynous (or very rarely semi-epigynous), with (3–)4–5(–8) sepals and (0–)4–5(–6, 12) petals per flower. The perianth parts are free in bud or occasionally form a calyptra or operculum or rupture irregularly at anthesis. In several genera the individual calyx lobes or the hypanthial remnants are deciduous after anthesis. Petals are white, cream, pale pink, or (rarely) deep pink or red. Stamens are usually numerous but, when few, the androecium may be diplostemonous, haplostemonous, or obhaplostemonous (i.e., a univerticillate androecium with only antipetalous stamens; Schmid, 1980). Stamens are generally free and attached directly to the hypanthium, but fascicled stamens occur in a few species of *Syzygium* sometimes segregated as *Pareugenia* (Schmid, 1972a). Most Myrtoideae have a secretory cavity at the apex of the anther connective but this feature is lacking in a handful of species in various genera (Schmid, 1972a). Carpels, when present, are 2 or occasionally 3–18 per flower, and the number of ovules per ovary is usually many, occasionally few, and very rarely one. General flower structure varies little among species as compared to other larger families, but flower size may vary by an order of magnitude.

Anther Development and Microsporogenesis

The anther is tetrasporangiate and dehiscence is by longitudinal slits. In *Gomidesia* the thecal margins are often strongly inrolled, so that the interior of the sacs and the pollen are only exposed over a small area at the apex (and often another small area at the base) of the anther. *Gomidesia* anthers have often been termed poricidal; however, they are more accurately described as longitudinally dehiscent and functionally poricidal. Terminally dehiscent anthers have also been reported in *Acmena.* The anther sacs, which are almost globose and somewhat divaricate, open by a terminal slit and are one of the diagnostic features of this genus (Merrill & Perry, 1938). Pollen grains of all Myrtoideae (and all Myrtaceae) studied to date are two-celled at anthesis (Schmid, 1984[1985]).

Pollen Grains

Patel et al. (1984) reviewed the palynological literature on the Myrtaceae. Pike's (1956) survey of 300 species in 71 genera remains the most comprehensive work on the subject to date. Although her study focused on the Leptospermoideae of the southwest Pacific area she also investigated representatives of the Myrtoideae, including some South American genera, and was forced to conclude "There appears to be no particular feature that separates the pollen of the Myrtoideae from that of the Leptospermoideae" (Pike, 1956: 46).

Barth and Barbosa (1972) confirmed the stenopalynous nature of the Myrtoideae on the basis of their survey of 140 species in 19 genera. They described myrtoid pollen as follows (translated from the Portuguese original with modern preferred terms (Punt et al., 1994) inserted [in brackets] after outmoded terms): "grains small to medium, oblate to peroblate, tricolporate with lalongate ora [endoapertures], goniotreme [angulaperturate] with triangular amb [polar view], surface of apocolpia and mesocolpia granular, smoother near the apertures. On average sexine is twice as thick as nexine 2 [endexine], which is constant in thickness. The sexine is tectate, the bacula [columellae] being responsible for the granular surface of the grains; undulations on the surface originate from the tectum. Nexine 1 [foot layer] is limited in occurrence; in general it is absent or reduced to fragments in grains with a thicker exine" (Barth & Barbosa, 1972: 468–469).

All these features common to the Myrtoideae are also characteristic of the Myrtaceae as a whole. Both Pike (1956) and Patel et al. (1984) recognized three pollen types in the Myrtaceae: (1) longicolpate, (2) syn- or parasyncolpate, and (3) brevi- or brevissimicolpate grains. All members of the Myrtoideae studied were reported to have grains of one or the other of the first two types, grains of type (3) being confined to certain members of the *Chamelaucium* group. However, Barth and Barbosa (1972) reported grains of all three types in the Myrtoideae and listed some 25 instances where both longicolpate and syncolpate grains were found in the same species, usually in the same collection, as most species in this study were represented by a single specimen. Similar variation was reported in about one third of the 18 species studied by Lieu and Melhem (1973), while most of the remaining species sampled had consistently longicolpate grains.

Pollen is released as free monads except in *Myrtus communis* L. and *Psidium cattleianum* Sabine (as *Psidium littorale* Raddi) where there is a mixture of free monads and tetrahedral tetrads (Patel et al., 1984). Dimorphic pollen occurs in association with cryptic dioecy in *Decaspermum parviflorum* (Lam.) A. J. Scott (Kevan & Lack, 1985) and in the South African species of *Eugenia* (van Wyk & Lowrey, 1988; van Wyk & Dedekind, 1985). Male flowers produce normal pollen grains and female (apparently hermaphrodite) flowers produce morphologically abnormal unviable pollen grains.

Stigma and Style Structure

Beardsell et al. (1993) described stigmas in the Myrtaceae as unspecialized and generally of the "wet" type, citing the Heslop-Harrison and Shivanna (1977) review of the receptive surfaces of the angiosperm stigma. In fact, Heslop-Harrison and Shivanna (1977) recorded dry stigmas with unicellular papillae in five of the seven genera of Myrtaceae studied, including all three of the myrtoid genera in the survey (*Acca* (as *Feijoa*), *Eugenia,* and *Syzygium*). Dry stigmas were also reported for the six genera studied by Proença and Gibbs (1994) (*Blepharocalyx, Campomanesia, Eugenia, Myrcia, Psidium,* and *Siphoneugena*) and in *Gomidesia* (Nic Lughadha, pers. obs.) and thus appear to represent the norm in the Myrtoideae.

Stigmas are undivided or very rarely divided. Bifid or occasionally trifid stigmas are reported in the African species *Eugenia ancorifera* Amshoff (Amshoff, 1974), *E. aschersoniana* F. Hoffm., and *E. mossambicensis* Engl. (Amshoff, 1958). Schmid (1980) drew attention to the style and stigma of *Campomanesia guazumifolia* (Cambess.) O. Berg, which has been variously described as "shortly bifid," "broadly capitate," and "peltate." Most Myrtoideae have punctiform or capitate stigmas. Proen-

Table 1. Correlations between stigma diameter, ovule number, and pollen tubes.*

Species (number of flowers per obs.)	Stigma diameter (mm)	Max. number of ovules	Max. number of pollen tubes
Blepharocalyx salicifolius (8 fls)	0.1	12	±35
Campomanesia pubescens (6 fls)	0.74	78	±20
Campomanesia velutina (4 fls)	0.57	29	±50
Eugenia dysenterica (3 fls)	0.1	8	±15
Myrcia linearifolia (3 fls)	0.1	4	17
Myrcia rhodosepala (3 fls)	0.1	6	10
Psidium firmum (3 fls)	0.65	298	±120
Siphoneugena densiflora (3 fls)	0.1	13	±15

* Adapted from Proença (1991).

ça (1991) reported both types in a study of eight species and went on to demonstrate a positive correlation between stigma diameter and ovule number (Table 1). This was explained in terms of the need for the stigma of a multi-ovulate flower to support more germinating pollen grains. The dioecious *Pimenta dioica* (L.) Merr. and the putatively dioecious *P. guatemalensis* (Lundell) Lundell are exceptions, having very low ovule numbers (1–4 per ovary) and large peltate stigmas. Proença (1991) argued that the females of these dioecious species no longer need to minimize stigma size in order to avoid deposition of self-pollen and consequent inbreeding depression (in the case of a self-compatible species) or occupation of all the ovules by self-pollen tubes and subsequent abortion of the pistil (in the case of a self-incompatible species) and suggested that expanded stigmas optimize pollen collection from the pollinator's body, the only pollen source for a totally female plant. *Carpolepis elegans* (Montrouzier) J. Wyndham Dawson, the only known dioecious Leptospermoideae, also has a large peltate stigma in contrast to the punctiform stigmas of its hermaphrodite congeners (Dawson, 1992).

Ovary Structure

The ovary comprises 2(3–18) fused carpels. The locules are generally multi-ovular, but the number of ovules is often reduced and very rarely each locule may contain only a single ovule. Axile placentation is the norm but parietal, basal, and apical placentation have also been reported (Schmid, 1980). Where placentation is axile a compitum (a passageway connecting the loculi) is often present. Carr and Carr (1961) commented that, because of their relationship to the stylar canal(s), such compita may increase the chance of fertilization where pollination is limited. Pollen tubes were observed growing through compita in *Siphoneugena densiflora* O. Berg and *Myrcia linearifolia* Cambess. (Proença, 1991).

Ovule Structure and Megagametophyte Development

The extremely uniform embryology of the Myrtoideae was noted by Mauritzon (1939). Recent reviews by Tobe and Raven (1983) and Beardsell et al. (1993) have shown that subsequent studies have added few genera to the list studied by Mauritzon and have done little to dispel the original impression of uniformity within the Myrtoideae.

Ovules of the Myrtoideae (as of the Myrtaceae as a whole) are generally described as anatropous, crassinucellate, and bitegmic. Mauritzon (1939) commented "I hardly exaggerate when I say that there is no other great family in the plant kingdom in which the ovules of the species so regularly have two invariably two-layered integuments." He then proceeded to describe the fusion of these two-layered integuments to form a single integument of four cell layers in material which he referred to as *Eugenia paniculata* Banks ex Gaertn. (almost certainly *Syzygium paniculatum* Gaertn.). Unitegmic ovules have also been reported in *Syzygium cumini* (L.) Skeels (Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium* (Lam.) DC.)), *Syzygium fruticosum* DC. (Roy, 1961 (as *Eugenia fruticosa* L.)), *Syzygium jambos* (L.) Alston (van der Pijl, 1934 (as *Eugenia jambos* L.)), *Syzygium malaccense* (L.) Merr. & L. M. Perry (van der Pijl, 1934; Roy, 1960 (as *Eugenia malaccensis* L.)), and *S. myrtifolium* (Roxb.) DC. (Roy, 1962 (as *Eugenia myrtifolia* Roxb.)). Van Wyk and Botha (1984) commented that those *Eugenia* species for which only a single integument has been described in the literature can probably all be referred to *Syzygium*. Tobe and Raven (1983) discussed the possible origin and significance of unitegmy in *Syzygium*. Few would dispute their conclusion that it represents a derived feature within the basically bitegmic Myrtales. However, their proposition that unitegmy "probably will be found in other genera when the family is better known embryologically" (Tobe & Raven, 1983: 86) has yet to be substantiated.

Mauritzon's generalization about myrtaceous integuments seems to hold true insofar as it concerns the inner integument: where this is distinct from the outer integument it is nearly always two cell layers thick (locally three cell layers thick in some South African *Eugenia* species (van Wyk & Botha, 1984)). However, the outer integument in the Myr-

toideae has proved more variable than Mauritzon's survey led him to suspect. Petit (1908, quoted in Mattos, 1989) reported 4 cell layers in the outer integument of *Luma apiculata* (DC.) Burret (as *Myrceugenia apiculata* (DC.) Nied.) and commented that the outer integument may comprise even more layers in some species of *Eugenia* judging by the considerable thickness of the integument of *Myrcianthes pungens* (O. Berg) D. Legrand and *Eugenia uniflora* L. (cited as *Eugenia pungens* O. Berg, and *Stenocalyx michelii* O. Berg, respectively). Van Wyk and Botha (1984) described an outer integument four to six layers thick over the greater part of its free length in their detailed study of South African *Eugenia*.

This latter group of *Eugenia* also seems to represent an exception to the generalization that ovules of the Myrtoideae (and the Myrtaceae) are anatropous. Van Wyk and Botha (1984) reported hemicampylotropous ovules (occasionally tending to be ana-campylotropous) and suggested that campylotropous ovules have frequently been taken as anatropous during cursory investigations.

In all Myrtoideae studied to date the micropyle is formed from both integuments. As in other Myrtaceae, embryo-sac formation in the Myrtoideae follows the *Polygonum*-type pattern and the antipodal cells are ephemeral (Tobe & Raven, 1983).

Flowering

Flowering Seasonality

Data on the time of initiation of flowering in the Myrtoideae have been compiled and discussed by Proença (1991) and Proença and Gibbs (1994). A tendency to flower at the dry/rainy season transition was distinguished, a pattern exhibited by 6 of the 8 species (in 6 different genera) studied by them in the Distrito Federal, central Brazil, and 7 out of 10 species of Myrtoideae investigated in other South American forest communities by other researchers (Frankie et al., 1983; Ferreira & Merona, 1987; Morellato et al., 1989). This pattern was clearly demonstrated in a floristic study of the Myrtaceae of the Serra do Cipó, Minas Gerais, Brazil, in which Kawasaki (1984, 1989) reported that the majority of the 50 species (in 11 genera) recorded for the area were found flowering in September and October (spring), after the first rains in the region. Two of these species had a second flowering period in February and March (late summer/early autumn), and a further five species flowered only during this latter period. In Costa Rican dry forest *Eugenia salamensis* Donn. Sm. was the only mass-flowering species (out of 21 mass flowerers studied) to bloom at the beginning of the wet season (Frankie et al., 1983). The other species (not Myrtaceae) bloomed during the long dry season. Ruiz and Arroyo (1978) reported flowering by *Eugenia* sp. at the beginning of the wet season in a Venezuelan deciduous forest. Proença and Gibbs (1994) proposed that flowering may be cued by abrupt increases in humidity, which are much more frequent at the dry/rainy season transition than during the remainder of the year. Landrum (1986) commented that most species of *Campomanesia* flower in the spring, usually in October in southeastern Brazil and adjacent regions. In contrast, most species of the temperate and subtropical South American genus *Myrceugenia* flower during the summer and autumn with a relatively small number of species flowering during late winter and spring (Landrum, 1981). Chilean Myrtaceae flower during the dry spring and summer (Landrum, 1988).

Southern African Myrtoideae exhibit a strong conformity to spring dry/wet season flowering, with 12 of the 15 species of *Eugenia* studied by van Wyk and Lowrey (1988) conforming to this pattern. The remainder flower in early summer (two species) or in winter (one species). Spring flowering is also reported as the norm in southern Australian Myrtaceae (Beardsell et al., 1993; O'Brien & Calder, 1993), though this generalization may be more applicable to the capsular dry-fruited Myrtaceae than to the Myrtoideae, as no specific examples from this latter group are cited. In fact, two detailed studies of Australian species of the genus *Syzygium* illustrate the variation in the time of flowering within this large genus. In Kuranda, northern Queensland, the rainforest tree *Syzygium tierneyanum* (F. Muell.) T. G. Hartley & L. M. Perry flowered in January (Hopper, 1980) while *S. cormiflorum* (F. Muell.) B. Hyland, another northern Queensland rainforest tree, had an extended flowering period ranging from at least late July to mid-November (Crome & Irvine, 1986). In Indonesia, however, at least one species of *Syzygium* does appear to demonstrate the dry/wet season transition spring flowering pattern discussed by Proença and Gibbs (1994): in Sulawesi trees of *Syzygium lineatum* (DC.) Merr. & L. M. Perry (as *Syzygium syzygioides* (Miq.) Merr. & L. M. Perry and subsequently corrected) flowered in February and March (spring) toward the end of what appeared to be "a fairly dry season"—precise information on climate was not available (Lack & Kevan, 1984). In the same area *Decaspermum parviflorum* (Lam.) A. J. Scott flowered in January and February, apparently toward the end of a short dry period (Kevan & Lack, 1985).

FLOWERING DURATION, PATTERN, AND SYNCHRONY

Meager though the data on flowering seasonality may appear, information on flowering strategies is scarcer still. Proença and Gibbs (1994) described four flowering strategies observed in the Myrtaceae of the Distrito Federal, central Brazil. Of these, three corresponded to types described by Gentry (1974) viz., "big bang," "cornucopia," and "steady state" flowering, and the fourth, for which they coined the term "pulsed bang," is a modification of the big bang strategy from which it differs in its discontinuity: flowering days may be followed by intervals of several days when no flowers are open. Such pulsed bang flowering was reported in *Myrcia rhodosepala* Kiaersk. and in *Blepharocalyx salicifolius* (Kunth) O. Berg in central Brazil. Kevan and Lack (1985) described a similar pattern in *Decaspermum parviflorum* in Sulawesi. In this species flowering occurred regularly once in every two or three days with all plants in synchrony over the peak blooming time from late January to mid-February. The total flowering period of ca. 4 weeks was, however, considerably shorter than the ca. 8-week periods estimated for the central Brazilian pulsed-bang species.

Also in Sulawesi, *Syzygium lineatum* had a total flowering period of approximately the same duration as the nearby *Decaspermum parviflorum* (ca. 4–5 weeks) but, as far as we could tell, appeared to exhibit a typical cornucopia pattern (Lack & Kevan, 1984). *Siphoneugena densiflora* in central Brazil also exhibited the cornucopia strategy with many flowers being produced per plant over a period of a month or so and a population flowering period estimated at 8 weeks.

The distinction between the cornucopia strategy and the steady state strategy in which relatively few flowers are produced each day over a long period of time may be somewhat arbitrary in some instances. The central Brazilian shrubs *Psidium firmum* Berg and *Campomanesia pubescens* (DC.) Berg, with flowering periods of ca. 12 weeks, were considered steady state (Proença & Gibbs, 1994). The Amazonian tree *Psidium acutangulum* DC. had an even longer flowering period. Flowering was reported all year round with relatively few flowers being produced from January to March (Falcão et al., 1992). Similar patterns were reported for other Amazonian fruit crops studied by these authors, including *Eugenia stipitata* McVaugh and *Myrciaria dubia* (Kunth) McVaugh (Falcão et al., 1988, 1989). The term steady state seems inappropriate for these latter species, as monthly totals for flower production exhibit spectacular peaks and dips. A better example of steady state flowering is provided by the northern Queensland species *Syzygium cormiflorum*, which has a rather long flowering period (> 14 weeks) and apparently relatively few flowers open per day. Crome and Irvine (1986) commented that "flowers are not numerous" and that their experimental program was limited by "insufficient flowers."

Syzygium tierneyanum, also from northern Queensland, appears to represent the opposite extreme of flowering strategy, viz., the classic big bang. The species is described as bursting into flower and reaching its peak over a 12-day period. Hopper (1980) counted 334 flowers per cubic meter of lower canopy and estimated that a 20-m plant could carry ca. 300,000 flowers at its seasonal peak. The central Brazilian species *Eugenia dysenterica* DC. and *Campomanesia velutina* (Cambess.) O. Berg also exemplify the big bang strategy, albeit on a smaller scale (Proença & Gibbs, 1994), as does *Eugenia salamensis*, a dry forest species in Costa Rica (Frankie et al., 1983).

Two Costa Rican dry forest shrubs, *Eugenia oerstediana* O. Berg and *Psidium guineense* Sw., exhibit a multiple bang strategy, flowering several times a year in synchronized flowering episodes lasting less than two weeks (Suarez & Esquivel, 1987).

LONGEVITY OF INDIVIDUAL FLOWERS

One-day flowers are the norm in the Myrtoideae. Species in which individual flowers last one day or less were reported from *Blepharocalyx*, *Campomanesia*, *Decaspermum*, *Eugenia*, *Myrcia*, *Myrciaria*, *Psidium*, *Siphoneugena*, and *Syzygium* (Hopper, 1980; Kevan & Lack, 1985; Peters & Vasquez, 1986/87; Proença & Gibbs, 1994). Stratton (1989) reported a mean floral longevity of 1.27 days, and a range of 1.1–1.5 days for three myrtaceous species in Costa Rican cloud forest. In this study of 110 species, in 35 families, taxonomic constraints at family level were the most important determinant of floral longevity, explaining 73% of the variance. Singh and Sehgal (1968) reported that the stigma of *Psidium guajava* L. is receptive for 2 or 3 days. Primack (1985), however, included the Myrtaceae in a list of families with long-lived flowers, which typically last 4–19 days. This generalization was very likely based on examples from the Leptospermoideae in which long-lived flowers appear to be common, e.g., flowers of *Leptospermum scoparium* J. R. Forst. & G. Forst. may last up to 3 weeks (Primack, 1980). Such longevity is rare in the Myrtoideae and where it occurs appears to be positively

associated with large flower size, e.g., *Syzygium cormiflorum* has flowers of ca. 4 cm in diameter, which do not brown until one week after anthesis (Crome & Irvine, 1986).

EFFECTS OF FIRE AND DROUGHT ON FLOWERING

In the Australian Myrtaceae flowering is not enhanced by fires. In fact, the flush of vegetative growth in recovering, fire-resistant species generally inhibits flowering for several seasons (Beardsell et al., 1993). In contrast, van Wyk and Lowrey (1988) reported that in southern Africa, grassland fires promoted new growth and flowering in the rhizomatous geoxylic suffrutex *Eugenia albanensis* Sond., and these authors considered that similar effects were likely in *E.* cf. *mossambicensis* and *E. pusilla* N. E. Br. Cesar (1980) reported three Myrtaceae (one *Campomanesia* sp. and two undetermined Myrtaceae) among 50 species that presented some form of fire-induced flowering in central Brazilian savanna grassland. *Eugenia myrcianthes* Nied. flowers very soon after burning in the same habitat (C. Proença, pers. obs.).

Sanaiotti and Magnusson (1995) studied the effects of annual fires on the production of fleshy fruits in a Brazilian Amazonian savanna. In *Eugenia biflora* DC. and *Myrcia sylvatica* (G. Mey.) DC. fruiting was dramatically reduced after fire, but recovery was rapid with fruiting reaching 50–90% of normal levels in the first year after burning and 50–100% in the second year.

Van Wyk and Lowrey (1988) considered drought conditions a major factor in delayed flowering in southern African *Eugenia*, while Falcão et al. (1988, 1989, 1992) reported flowering periods coinciding with precipitation minima in three Amazonian species, i.e., *Eugenia stipitata*, *Myrciaria dubia*, and *Psidium acutangulum*.

Breeding Systems

DICHOGAMY

Beardsell et al. (1993) commented that all hermaphroditic species of the Myrtaceae studied so far, except for one protogynous species of *Verticordia*, have protandrous flowers, although there may be some overlap of male and female phases providing potential for self-pollination. Intervals of days or even weeks separating male and female phases are not uncommon in the Leptospermoideae, but the potential for such conspicuous protandry is significantly reduced in the Myrtoideae where flowers are generally short-lived. Furthermore, the detection of dichogamy in the Myrtoideae is rendered more difficult by the dry nature of the stigma, which does not permit visual assessment of receptivity.

From a theoretical viewpoint it seems unlikely that temporal separation of male and female functions should be widespread but undetected among the Myrtoideae with short-lived flowers which offer only pollen as a reward. Female-phase flowers would offer nothing to reward visitors and, as Renner (1989) commented, only mimicry or deception might account for visits to such flowers. That dichogamy should co-occur with nectar production seems more likely and this does in fact appear to be the case in at least three of the four genera where the existence of dichogamy has been postulated.

Dichogamy seems most likely to occur in *Syzygium*, where many species offer nectar as a reward; interestingly, this genus includes species with relatively long-lived flowers possibly affording more scope for temporal separation of male and female functions. In the context of the Myrtoideae the flowers of *Syzygium cormiflorum*, as already mentioned, are remarkably long-lived: styles do not brown until, on average, a week after anthesis, and they are not shed until about three weeks later (Crome & Irvine, 1986). According to these authors a flower could be successfully pollinated at anthesis, but they were unable to tell whether the stigma was actually receptive on the first day or whether the pollen retained viability until the stigma matured later. Thus protandry is possible but not confirmed in this species.

The only reliable report of protandry in the Myrtoideae that we have encountered to date is that of Grifo (1992) for *Myrcianthes*. In some species of this genus the stigma remains introrsely curved until after the anthers have released much of the pollen through longitudinal slits and are leaning outwards, away from the now erect and apparently receptive stigma. Grifo (1992) also reported nectar production in *Myrcianthes*—see Attractants and Rewards below.

Peters and Vasquez (1986/87) have documented protogyny in *Myrciaria dubia*, where the stigma is exserted first and the filaments of the numerous anthers expand later. These authors stated that anthesis occurs early in the morning, that the flowers are receptive to pollination for a period of 4–5 hours, and that by the time the anthers emerge to release the pollen the stigma is no longer receptive to pollination. The method of assessment of stigma receptivity was not discussed but in the accompanying diagram the stigma appears shrivelled in the flower with erect stamens. After pollination the stamens start to wilt and the whole hypanthial cup,

with sepals, petals and stamens, abscisses on the following day, leaving only the ovary. Grifo (1992) commented that the monotypic *Amomyrtella* is also decidedly protogynous. The large peltate stigma of this species is exserted before the petals unfold (herbarium label for *Solomon 11018*).

Stylar extension post-anthesis is common in the Leptospermoideae. It appears to coincide with the onset of stigma receptivity and has been variously interpreted as a mechanism to favor outcrossing (Moncur & Boland, 1989) or as a mechanism to reduce interference from self-pollen (Lloyd & Webb, 1986; Webb & Lloyd, 1986). The phenomenon appears to be rarer in the Myrtoideae but has been reported from two species of *Syzygium*. In the flowers of *S. cormiflorum* the style expands to maximum length 4–5 days after opening and after the stamens are shed (Crome & Irvine, 1986). In contrast, in the one-day flowers of *S. lineatum*, the style reaches its full length 4 to 6 hours after anthesis, often while the anthers still have much pollen on them (Lack & Kevan, 1984).

ANDROMONOECY AND DIOECY

Andromonoecy, which is common in the Leptospermoideae (Beardsell et al., 1993), has not been detected in the Myrtoideae. Interestingly, Beardsell et al. (1993) suggested that andromonoecy in the Australian Myrtaceae (Leptospermoideae) may represent a response to soils of low fertility and to drought, allowing optimal resource allocation for reproduction. The Myrtoideae, in contrast, though tolerant of poor soils appear to be drought avoiders, reaching their maximum ecological importance (as estimated by density and/or basal area) in areas of South America where there is a combination of coolish temperatures, a steady supply of water, and a poor, weakly acidic soil (Proença, 1991).

The term cryptic dioecy has been applied to dioecious breeding systems in which one or both of the functionally unisexual morphs appear to have perfect hermaphroditic flowers, making the dioecious condition difficult to detect (Mayer & Charlesworth, 1991). In populations of most cryptically dioecious species, plants with staminate flowers (male) co-exist with apparently perfect-flowered but functionally pistillate (female) plants whose anthers produce sterile or abnormal pollen, or are indehiscent. This situation is sometimes mistaken for androdioecy, in which functionally male and functionally hermaphrodite individuals co-exist.

Nic Lughadha (1994) summarized current knowledge on dioecy in the Myrtaceae, which has until recently been considered a relatively rare phenomenon (van Wyk & Lowrey, 1988). In the Myrtoideae, cryptic dioecy has been reported in *Pimenta dioica* (Chapman, 1964), in *Decaspermum parviflorum* (Kevan & Lack, 1985), and in all 15 species of *Eugenia* native to South Africa (van Wyk & Lowrey, 1988). With the exception of *Pimenta dioica*, which has structurally hermaphroditic flowers in both sexes, all of these species have male flowers with greatly reduced pistils, while female flowers appear perfect but generally have fewer stamens whose anthers do not produce viable pollen. In the typically small myrtaceous flower with its many stamens, both types of cryptic dioecy (apparently hermaphrodite and apparently androdioecious) may easily be overlooked by the casual observer and are probably more common than the few literature reports suggest.

Reduced styles and abortive ovaries have been reported for *Pimenta guatemalensis* (Lundell, 1968) and for three species of *Calyptranthes*, *C. fasciculata* O. Berg (Berg, 1857), *C. longifolia* O. Berg, and *C. speciosa* Sagot (McVaugh, 1958). In the *Flora of Peru*, McVaugh (1958) also noted short styles and apparent imperfect development of the hypanthium in *Myrcia aliena* McVaugh and suggested that this species may be partially or completely dioecious. A further two imperfect flowered species are among the thirty species of *Myrcia* described as new by McVaugh (1969). *Myrcia imperfecta* McVaugh and *M. myriantha* McVaugh (both from Mount Ayanganna, Guyana) were each based on a single collection with male flowers only and no vestige of a style. McVaugh commented that this was a condition rarely noted in *Myrcia* and that its significance was unknown, though the imperfect flowers of *M. imperfecta* could be abnormal. *Myrcia almasensis* Nic Lughadha from the Pico das Almas, Brazil, was based on apparently male material with a vestigial style and brought to four the total number of putatively dioecious species of *Myrcia*. Of course the possibility that some of these collections may represent andromonoecious species cannot as yet be discounted. Interestingly, many of these putatively dioecious neotropical Myrtoideae are from high-altitude areas. Sobrevila and Arroyo (1982) have discussed the abnormally high incidence of dioecy in a Venezuelan montane cloud forest as compared to other tropical forest communities.

Classical dioecy, where female flowers lack stamens completely, is unlikely to occur in the Myrtoideae. In flowers offering pollen as a sole reward to pollinators, which is the case for most Myrtoideae, selection tends to favor female flowers which mimic male flowers by retaining stamens, even though the pollen therein may be sterile (Lloyd, 1982). A possible mechanism for the evolution of

dioecy in pollen-only taxa is outlined under Attractants and Rewards below.

Dioecy is unknown in the Australian Myrtaceae (Beardsell et al., 1993), and we consider it highly improbable that it has been extensively overlooked there. The only published example we have encountered of dioecy in the Leptospermoideae occurs in the small genus *Carpolepis*, which is endemic to New Caledonia (Dawson, 1992). *Carpolepis elegans* is dioecious and, apparently, more or less cryptically so. Male flowers include fertile stamens, a morphologically normal, but non-functional ovary, a full-length style, and a peltate stigma; female flowers are similar but the stamens are replaced by recurved staminodes whose anthers bear no pollen. The other two species of *Carpolepis* bear hermaphrodite flowers with punctiform stigmas. Dioecism has also been discovered in some species of the Myrtoideae of New Caledonia, and these are shortly to form the basis of a new genus (J. W. Dawson, pers. comm.).

The fact that dioecy is extremely rare in the Leptospermoideae yet appears to have arisen independently on at least half a dozen different occasions in the Myrtoideae can be interpreted as further evidence in support of the non-random association between dioecy and dispersal mode, which was described and discussed by Bawa (1980) and Givnish (1980, 1982). These authors argued that unisexuality is more likely to establish itself in taxa with large few-seeded animal-dispersed fruits than in taxa with other modes of dispersal. In species that produce nutrient-rich fruit an increase in female reproductive effort produces a disproportionate increase in female fitness due to selection for spatial and temporal peaks in fruit production. They consider that such an advantage to increasing female effort could, under certain circumstances, favor individuals that invest only as females or only as males.

OUTCROSSING RATES

In most Myrtoideae, especially the small-flowered species, many flowers are produced per tree per flowering day. The potential for geitonogamy would therefore seem great. However the low PERS values [Pre-emergent reproductive success, the percentage of all ovules maturing into seeds expressed as: % natural fruit set × no. of seeds per fruit/no. of ovules per fruit, Wiens et al., 1987] typically found in the Myrtoideae (Proença & Gibbs, 1994; Nic Lughadha, unpublished data) are suggestive of predominantly outbreeding species. Electrophoretic studies have demonstrated the existence of high outcrossing rates in various species of *Eucalyptus* and *Melaleuca* with similar flowering patterns (Phillips & Brown, 1977; Moran & Bell, 1983; Griffin et al., 1987; Butcher et al., 1992). Beardsell et al. (1993) interpreted these high levels of outcrossing in spite of ample opportunities for geitonogamy as reflecting the operation of a barrier to self-pollination such as self-incompatibility. Proença (1991) suggested that high levels of outbreeding could be maintained even in self-compatible species through flowering strategies that favor trap-lining or opportunistic behavior by pollinators. In cultivated *Psidium guajava*, a relatively low level of outcrossing of 25–41% (mean = 36%) was reported by Soubihe Sobrinho and Gurgel (1962).

SELF-INCOMPATIBILITY

Beardsell et al. (1993) considered that self-incompatibility is probably widespread in the Myrtaceae. They cited cases ranging from partial self-incompatibility to complete self-sterility with no seed production after selfing. No myrtoid examples of self-sterility were reported, but they considered it likely that the same mechanism of self-incompatibility operates throughout the Myrtaceae and acknowledged the need to examine more species in order to determine whether reduced seed-set after selfing is due to the expression of lethal recessive genes in the zygote or to a late-acting self-incompatibility system. The latter explanation was favored by Proença and Gibbs (1994) in their study of the reproductive biology of central Brazilian Myrtoideae. Of the eight species studied by these authors, three (*Blepharocalyx salicifolius*, *Campomanesia velutina*, and *Siphoneugena densiflora*) were apparently strictly self-incompatible and set no fruit when selfed. A further two species (*Myrcia linearifolia* and *Campomanesia pubescens*) exhibited partial self-incompatibility with ISI values [Index of Self-Incompatibility, expressed as the ratio of fruit set from selfed vs. crossed flowers] of 0.12 and 0.09, respectively. Self-pollen tubes were observed to penetrate ovules in all of these species and no differences were detected between self- and cross-pollinations with respect to the mean number of penetrated ovules per flower at 24, 48, or 72 hours after pollination. The time of abscission of selfed pistils varied between species from one week to one month after pollination, but rejection was synchronous within species, and no ovary enlargement was detected in crossed or selfed pistils up to the time of abscission of the latter. This represents the most detailed study of "self-incompatibility" in the Myrtoideae published to date but, as no material was fixed beyond 72 hours after pollina-

tion, we can only speculate as to the nature of the rejection mechanism in operation. More recent studies on *Gomidesia* have included fixations up to 28 days after pollination, and results obtained to date suggest that preferential outcrossing is sustained by a post-zygotic mechanism or effect (Nic Lughadha, unpublished data).

Complete self-sterility has also been reported in *Eugenia* sp. in secondary deciduous forest in Venezuela (Ruiz & Arroyo, 1978), in *Eugenia* sp. (presumably different) in montane cloud forest in Venezuela (Sobrevila & Arroyo, 1982), and in *Syzygium lineatum* in Sulawesi, Indonesia (Lack & Kevan, 1984). Bullock (1985) reported almost complete self-incompatibility in Mexican *Psidium sartorianum* Nied. (ISI 0.02). However, in none of these cases is any indication given of the timing or nature of the reproductive barriers operating after self-pollination.

Reports of self-compatibility in Myrtoideae are almost as numerous as those of self-incompatibility. Proença and Gibbs (1994) recorded three completely self-compatible species (*Eugenia dysenterica, Myrcia rhodosepala,* and *Psidium firmum*) that set statistically equal numbers of fruits after self- and cross-pollination. For the cultivated guava, *Psidium guajava,* self-pollination in isolated trees has been registered between 64% and 90% (Soubihe Sobrinho & Gurgel, 1962). In Peru, *Myrciaria dubia* showed 91% fruit set after geitonogamous pollination (Peters & Vasquez, 1986/87). In Venezuela, *Myrcia fallax* (Rich.) DC. showed significantly diminished fruit set after self-pollination as compared to cross-pollination; however, its ISI of 0.24 exceeded the threshold value of 0.2 arbitrarily set for self-incompatible species (Bawa, 1974; Sobrevila & Arroyo, 1982), and so this species was classed as self-compatible. *Syzygium cormiflorum* from northern Queensland also exhibited partial self-compatibility with 18–36% fertilization (estimates based on ovule enlargement) in self-pollinated flowers and 72.7–86.7% fertilization in cross-pollinated flowers (Crome & Irvine, 1986). In another northern Queensland tree species, *Syzygium tierneyanum,* bagged inflorescences set fruit in the absence of cross-pollination (Hopper, 1980). Beardsell et al. (1993) interpreted this result as demonstrating autogamy (in the sense of automatic self-pollination of a self-compatible species) but did not discuss the possibility of apomixis. Chantaranothai and Parnell (1994) obtained similar results in a study of breeding systems of Thai species of *Syzygium.* They found that all four species studied in detail were apparently self-compatible with self-pollination appearing to enhance seed-set. However, they further demonstrated that two of these species were actually apomictic (see below). Purseglove (1968) documented self-fertility in *Psidium guajava.* Schroeder (1947) reported results ranging from complete self-compatibility to almost complete self-incompatibility in different varieties of *Acca sellowiana* (O. Berg) Burret (as *Feijoa sellowiana* O. Berg).

APOMIXIS

Davis (1966) reported apomixis as occurring widely within the Myrtoideae. Where apomixis occurs it is generally by adventitious embryony, although there is some evidence indicating the possibility of apospory. The resulting polyembryony is discussed in more detail under Embryo and Seed Development (see below).

Rye (1979) postulated a positive correlation between the widespread occurrence of apomixis in the Myrtoideae and the high frequency of polyploidy in this group, but commented that the only specific example was *Syzygium jambos* (cited as *Eugenia jambos*). A further example is *Syzygium cumini,* which exhibits adventitious polyembryony (though apparently not consistently: Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium*); Tiwary, 1926 (as *Eugenia jambolana* Lam.); van der Pijl, 1934 (as *Eugenia cumini* (L.) Druce); Chantaranothai & Parnell, 1994) and in which several authors reported varying levels of polyploidy (Mehra, 1976; Bir et al., 1980; Singhal & Gill, 1984; Singhal et al., 1984, 1985; Gill et al., 1989: as *E. jambolana* in each case, gametophytic counts 11, 22, and 33, sporophytic counts 22, 44, and 66). Whether this association extends to other polyembryonic members of the genus *Syzygium* and, more importantly, whether it is continued outside the genus remains to be investigated. *Luma apiculata,* the only other polyembryonic species of the Myrtoideae for which chromosome counts are available, lends no support to Rye's hypothesis as it is reported to have $n = 10$ (Titow de Tschischow, 1956), or about $2n = 22$ (Landrum, 1981). However, as there is circumstantial evidence that polyploidy may not be ubiquitous in this species, it is possible that these diploid counts may derive from non-polyembryonic material. The correlation cannot be tested further in the absence of chromosome counts for any other myrtoid genera in which polyembryony has been documented.

Pollination Biology

ATTRACTANTS AND REWARDS

Petals and/or stamens may act as the visual attractants in flowers of the Myrtoideae, but the sta-

mens are generally the most conspicuous structures in the open flower. Scent also appears to play a role in attraction. The odors produced are generally described as sweet but flowers of *Syzygium cormiflorum* have a faint unpleasant smell (Crome & Irvine, 1986). Grifo (1992) described the flowers of *Myrcianthes* as smelling either sweet and similar to an apple-blossom or rather sour and similar to "well-seasoned sneakers." Chantaranothai and Parnell (1994) found that floral buds of *Syzygium jambos* and *S. megacarpum* (Craib) Rathakr. & N.C. Nair were sweetly fragrant during the period of swelling before anthesis. In southern African *Eugenia* species van Wyk and Lowrey (1988) did not discover any osmophores but found that the strong sweet odor was emitted either by the anther tisue and/or by the pollen grains.

Pollen is the principal reward available to visitors of most Myrtoideae flowers. Van Wyk and Lowrey (1988) found that the pollen of southern African *Eugenia* tested positive for lipids (in the form of oil droplets) and negative for starch. Moncur (1988) commented that sugars in pollen are pollinator rewards in *Acca sellowiana* (as *Feijoa sellowiana*). In several dioecious species, such as the southern African *Eugenia* and *Decaspermum parviflorum*, female flowers produce non-viable pollen-like material which may represent an important resource to insect pollinators (Kevan & Lack, 1985; van Wyk & Lowrey, 1988). Kevan and Lack commented that *D. parviflorum* is unusual among dioecious species in presenting pollen (and sterile pollen) as the main food reward and cited *Vitis* and *Solanum* as other examples of this phenomenon. However, pollen-only flowers also occur in other dioecious species such as *Actinidia chinensis* Planch. (Schmid, 1978), *Rosa setigera* Michx. (Kevan et al., 1990), and *Saurauia veraguasensis* Seem. (Haber & Bawa, 1984). It is noteworthy that female flowers of these species accrue neither of the major advantages proposed by Bawa (1980) for female flowers of dioecious species: they must still allocate resources to the production of stamens and sterile pollen and still run the risk of their stigmas becoming clogged with their own sterile pollen. This could be interpreted as an indication that the avoidance of inbreeding may represent a more important selective force in the maintenance of dioecy in these species than does the reallocation of reproductive resources (Mayer & Charlesworth, 1991). However, it should be borne in mind that reallocation of resources may take place on a whole-plant level, with male plants producing a more prominent floral display, more flowers, and/or more pollen per flower than female plants. This is certainly true of *D. parviflorum* (Kevan & Lack, 1985), and there is circumstantial evidence that it may be the case in other putatively dioecious Myrtoideae (Nic Lughadha, 1994). Givnish (1980) discussed the potential role of sexual selection in the evolution of dioecy in pollen-only taxa. Where pollen is the only reward then disproportionately many pollinators may be attracted to plants with heavy pollen loads. This advantage could drive the evolution of dioecy if male and female flowers mimic each other, as is the case in all dioecious Myrtoideae known to date (see discussion of dioecy above).

Besides the pollen and sterile pollen offered as the principal reward, *Decaspermum parviflorum* is also reported to produce minute quantities of nectar (Kevan & Lack, 1985). Most other reliable reports of nectar production that we have encountered refer to species of the genus *Syzygium*. Schmid (1972b) described an ovarian annular nectary in *S. aromaticum* (L.) Merr. & L. M. Perry, *S. jambos*, *S. malaccense*, and *S. paniculatum* and cited Werth's (1901) account of the secretion of nectar in copious amounts into the concavity formed by the depressed top of the ovary in flowers of *S. jambos* (as *Jambosa vulgaris* DC.). Crome and Irvine (1986) measured copious but variable flow of weak nectar in *S. cormiflorum*. Small quantities of nectar of rather high sugar content are produced in flowers of *S. lineatum* (as *S. syzygioides*; Lack & Kevan, 1984). Nectar production is also reported from *S. tierneyanum* (Hopper, 1980) and *S. samarangense* (Blume) Merr. & L. M. Perry (Chantaranothai & Parnell, 1994).

Studies of genera of Myrtoideae other than *Syzygium* have generally failed to find any evidence of nectar production. Nectar is absent in flowers of southern African *Eugenia* species (van Wyk & Lowrey, 1988) and, apparently, in most South American Myrtoideae (Landrum, 1986; Proença & Gibbs, 1994; Nic Lughadha, unpublished data). Exceptions include the report by Pirani and Cortopassi-Laurino (1993) of bees collecting pollen and nectar from flowers of *Plinia glomerata* (O. Berg) Amshoff and that of Peters and Vasquez (1986/87) on nectar production in *Myrciaria dubia*. The other notable exception is the genus *Myrcianthes*, in which sweet-tasting nectar is secreted at the base of the staminal disk (Grifo, 1992). Grifo's descriptions of visitor behavior indicate that nectar is the principal reward offered by these species. Small insects may approach the flowers and feed on the nectar while entirely avoiding the numerous stamens, but larger insects become covered with pollen as they brush the anthers in search of nectar.

Nectar is widespread in the Leptospermoideae, and the nectar-producing *Chamelaucium* group

emerged as sister to the Myrtoideae in cladistic analyses by both Johnson and Briggs (1984) and Grifo (1992) (along with the *Leptospermum* group in the former analysis). Grifo's (1992) cladistic analysis also indicated that *Myrcianthes* is "much more closely related to *Syzygium* than previously supposed" and that these genera are basal to the Eugeniinae in the Neotropics. We can therefore hypothesize that nectar production is basal in the Myrtaceae with the numerous pollen-only genera of the Myrtoideae arising as a result of secondary loss(es) of this facility. Renner (1989) has proposed a similar scenario to explain the distribution of nectar production among the neotropical melastomes. Her observation that the Melastomataceae that offer nectar are pollinated by a broader range of pollinator classes than the pollen-only species seems also to hold true for the Myrtaceae on the basis of the evidence available to date.

The role of the secretory cavity at the apex of the anther connective does not appear to have been investigated in any member of the Myrtoideae. In *Thryptomene calycina* (Lindl.) Stapf, a member of the *Chamelaucium* alliance (Leptospermoideae s.l.), Beardsell et al. (1989) demonstrated that the anther connective glands secrete a lipid-rich fluid which solidifies and serves as a food reward for pollinating insects. Although a similar role is possible for the anther connective glands of the Myrtoideae it seems unlikely that any visitor small enough to be attracted to the minute quantities of secretion that these glands might afford would contact the stigma regularly while collecting. Renner (1989) discussed a comparable paradox offered by the staminal glands of *Mouriri* (Memecylaceae) and noted Morley's (1976) suggestion that these glands may be involved in odor production. Van Wyk and Lowrey's (1988) observations on fragrant anthers and pollen in southern African *Eugenia* represent the only evidence we have encountered to support the hypothesis of an odor production role for the anther connective glands in the Myrtoideae. Of course, another possibility is that these structures serve no function in the flowers of the Myrtoideae and are simply vestigial remnants of an organ which is more or less ubiquitous in the Myrtaceae. The scattered examples of species whose anthers lack secretory cavities undoubtedly represent secondary losses of this feature.

The role of petals as an attractant and reward to visitors to *Acca* and *Myrrhinium* is discussed under Bird Pollination below.

BEE POLLINATION

Bees (Apoidea) appear to be the most common pollinators of Myrtoideae, as they are of Myrtaceae as a whole. There is a strong association between the Myrtaceae and the short-tongued Colletidae, which are considered to be the most primitive flower-visiting bees (Michener, 1979). This relationship is most notable and best documented in Australia where nearly half of the bee species belong to the Colletidae and most of these are restricted to or collect pollen primarily from flowers of Myrtaceae (Armstrong, 1979). These include *Eugenia* and *Syzygium* as well as numerous non-myrtoid genera. Bees reported to collect pollen from *Eugenia* and/or *Syzygium* include *Euryglossina* and *Hylaeus* (Colletidae) as well as *Homalictus* and *Lasioglossum* (Halictidae) (Michener, 1965). When current taxonomic concepts are applied, most of these records are referrable to the genus *Syzygium*; only one species of *Eugenia* s. str. occurs in Australia (Hyland, 1983).

Proença and Gibbs (1994) suggested that the Myrtaceae–Colletidae association, so striking in Australia, probably exists to some extent in the Neotropics. They cited two neotropical examples of this association, viz., rapid pre-dawn pollen removal from *Eugenia salamensis* by *Ptiloglossa* spp. (Colletidae: Diphaglossinae) in Costa Rica (Frankie et al., 1983) and pollination of *Siphoneugena densiflora* by *Ptiloglossa* sp. in central Brazil (Proença, 1992). Colletidae are not particularly common in the Neotropics: e.g., in central Brazil, where the Proença and Gibbs study was carried out, only 5% of bee species are Colletidae (A. Raw, unpublished list based on 12,000 collections). Therefore one could argue that such reports are unlikely in the absence of some degree of association. However, a careful compilation of 33 reports of bee visitation in neotropical Myrtoideae (Table 2) showed that most registered visits are by Apidae: Meliponinae (14), followed by Apidae: Bombinae (9), Halictidae (4), Anthophoridae (4), Colletidae (2). In defense of the neotropical Myrtaceae–Colletidae association, it should be noted that both reports were of pre-dawn visitation, so that this phenomenon could be widespread but largely overlooked in studies based purely on diurnal observations.

The first report of buzz-pollination in the Myrtaceae was published by Proença (1992). She described buzz-pollination in *Siphoneugena densiflora* by *Ptiloglossa* sp., in *Myrcia torta* DC. (as *M. dictiophylla* (O. Berg) J. R. Mattos & D. Legrand) by *Augochloropsis*? sp. (Halictidae), and in *Myrcia rhodosepala* and *Blepharocalyx salicifolius* by *Bombus* spp. (Apidae: Bombinae). *Bombus* spp. (including *B. atratus* and *B. morio*) were considered the principal pollinators of a further five species of central Brazilian Myrtaceae (*Campomanesia pubescens, C.*

Table 2. Species of neotropical Myrtoideae with presumed pollinators or insect visitors to flowers.

Species	Visitors	Behavior	Reference
Blepharocalyx salicifolius	Apidae: Bombinae Apidae: Meliponinae Halictidae	"visitors"	Proença & Gibbs (1994)
Campomanesia pubescens	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
Campomanesia velutina	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
Eugenia dysenterica	Apidae: Bombinae Apidae: Meliponinae	"visitors"	Proença & Gibbs (1994)
Eugenia salamensis	Colletidae	"foraging"	Frankie et al. (1983)
Eugenia stipitata	Apidae: Meliponinae	"visiting"	Falcão et al. (1988)
Eugenia sp. 1	Apidae: Meliponinae	"aggressive behavior"	Roubik (1989)
Eugenia sp. 2	Halictidae	"visits"	Ruiz & Arroyo (1978)
Eugenia spp.	Apidae: Meliponinae	"collect pollen"	Absy & Kerr (1977)
Myrcia linearifolia	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
Myrcia rhodosepala	Apidae: Bombinae Anthophoridae: Xylocopinae	"pollinators"	Proença & Gibbs (1994)
Myrcia torta	Halictidae ?	"pollinators"	Proença & Gibbs (1994)
Myrcia sp.	Apidae: Meliponinae	"pollen in honey"	Vit & D'Albore (1994)
Myrciaria dubia 1	Apidae: Meliponinae	"visiting"	Falcão et al. (1989)
Myrciaria dubia 2	Apidae: Meliponinae	"pollinators"	Peters & Vasquez (1986/87)
Pimenta dioica	Anthophoridae: Xylocopinae Anthophoridae: Anthophorinae Halictidae	"visiting"	Chapman (1965)
Plinia cauliflora	Apidae: Meliponinae	"intensive exploitation"	Guibu et al. (1988)
Plinia glomerata	Apidae: Bombinae Apidae: Meliponinae	"foraging"	Pirani & Cortopassi-Laurini (1993)
Psidium acutangulum	Apidae: Meliponinae	"visiting"	Falcão et al. (1992)
Psidium firmum	Anthophoridae: Xylocopinae Apidae: Bombinae	"presumptive pollinator"	Proença & Gibbs (1994)
Psidium guajava 1	Apidae: Meliponinae Apidae: Bombinae	"foraging"	Camillo & Garófalo (1989)
Psidium guajava 2	Apidae: Meliponinae	"intensive exploitation"	Guibu et al. (1988)
Siphoneugena densiflora	Colletidae	"presumptive pollinator"	Proença (1992)
Myrtaceae indet. spp.	Apidae: Meliponinae	"pollen in honey"	Vit & D'Albore (1994)

Note. Visits by honeybees, introduced to the Neotropics, are excluded from this table.

velutina, Eugenia dysenterica, Myrcia linearifolia, and *Psidium firmum*), but no buzzing behavior was noted during observation of these species. The same species of *Bombus* exhibited a preference for *Psidium guajava* in secondary vegetation in southeastern Brazil (Camillo & Garófalo, 1989). *Bombus* spp. were reported to collect pollen and nectar from *Plinia glomerata* in São Paulo (Pirani & Cortopassi-Laurino, 1993). Visits by *Melipona quadrifasciata, Tetragonisca angustulata* (both Apidae: Meliponinae), and *Apis mellifera* were also recorded. Guibu et al. (1988) documented intensive exploitation of Myrtaceae by *Melipona quadrifasciata.* They listed *Psidium guajava* s.l. and *Plinia cauliflora* (Mart.) Kausel s.l. (as *Myrciaria cauliflora* (Mart.) O. Berg s.l.) among the species visited by these bees in São Paulo, Brazil.

Other species of the bee genus *Melipona* may be important pollinators of Myrtaceae in Amazonian Brazil. *Melipona rufiventris* and *M. seminigra* collected pollen of *Eugenia* spp. and other unidentified Myrtaceae near Manaus (Absy & Kerr, 1977; Absy et al., 1980). In the same area Falcão et al. (1988, 1989, 1992) recorded *Melipona lateralis* and

M. pseudicentris visiting cultivated *Eugenia stipitata, Myrciaria dubia,* and *Psidium acutangulum.* In the nearby Reserva Ducke, Roubik (1989) observed aggressive behavior of several species of *Trigona* (Meliponinae) on *Eugenia* sp. In Peru *Myrciaria dubia* is commonly pollinated by *Melipona fuscopilara* and *Trigona postica* (Peters & Vasquez, 1986/87). A recent study of pollen spectra in the honey of 48 species of *Melipona* in Venezuela (Vit & D'Albore, 1994) provides additional evidence of the importance of Myrtaceae to these bees: Myrtaceae spp. and *Myrcia* sp. were respectively the fifth and eighth most common pollen types in a list of 13. Ruiz and Arroyo (1978) reported visits to a Venezuelan *Eugenia* sp. by *Augochloropsis fulvofimbriata* (Halictidae) and by *Apis mellifera* and *Trigona testiceicornis* (Apidae).

Chapman (1965) saw solitary bees belonging to the genera *Ceratina* (Anthophoridae, Xylocopinae), *Exomalopsis* (Anthophoridae, Anthophorinae), and *Halictus* (Halictidae), as well as honeybees, visiting flowers of *Pimenta dioica* for pollen in Jamaica.

In a population of *Decaspermum parviflorum* in a forest clearing in Indonesia, Kevan and Lack (1985) recorded vigorous pollen collection during a 45-minute peak period by a variety of bees, mostly *Apis dorsata* (Apidae: Apiinae) and *Nomia* spp. (Halictidae: Nomiinae). *Nomia* and *Trigona* continued to glean during the rest of the day and perfunctory visits by *Xylocopa* spp. were also reported. In a nearby forest *Syzygium lineatum* (as *Syzygium syzygioides* and subsequently corrected) was visited sparingly and mainly for nectar (Lack & Kevan, 1984). Another study notable for the paucity of potential pollen vectors was that of van Wyk and Lowrey (1988). These authors provisionally considered that the 15 southern African species of *Eugenia* studied might be bee-pollinated, as honeybees were observed visiting *Eugenia* spp. in Pretoria and were also active in natural populations of *Eugenia capensis* Harv.

BIRD POLLINATION

Bird pollination appears to be much less frequent in the Myrtoideae than in the Leptospermoideae. Ford et al. (1979) reported six species of birds visiting three species of *Syzygium* in Australia, but in no case was a bird actually seen to be carrying pollen. Honeyeaters were reported as the most commonly observed vertebrate visitors to flowers of *Syzygium cormiflorum* and *S. tierneyanum* in Australia (Hopper, 1980; Crome & Irvine, 1986). Hopper (1980) suggested that honeyeaters may be the most important pollinators of *S. tierneyanum* but acknowledged that the role of bats was neglected in his study. Crome and Irvine (1986) demonstrated experimentally that in *S. cormiflorum* birds were far less effective pollinators than bats, accounting for less than 25% of all successful pollinations. Both of these species have white or cream flowers, but Ford et al. (1979) noted a tendency for red stamens among large-flowered, bird-pollinated Australian Myrtaceae in general (mostly Leptospermoideae).

Two small neotropical myrtoid genera, *Acca* and *Myrrhinium,* have stiff red stamens reminiscent of those of many Australasian bird-pollinated Myrtaceae. Landrum (1986) noted that there is no nectar in the fresh flowers of *Acca sellowiana* and that in both genera the petals change color and become sweet and juicy just as the anthers dehisce. There are various reports of visiting birds eating the petals of *Acca sellowiana* (Kiaerskov, 1893; Knuth, 1906; McGregor, 1976; Vogel et al., 1984). In view of their isolated position within the Myrtoideae, Landrum (1986) hypothesized that the use of petals as an attractant in these two closely related genera (which he called the *Myrrhinium* complex) is very ancient. Schroeder (1947), however, observed extensive bee visitation in *Acca sellowiana* cultivated in California and found that flowers so visited set fruit ca. 16 times as well as flowers protected from visitation. Free (1993) also reported that bees are frequent visitors to the flowers of this species and assumed that they were responsible for most of the pollinations. In *Myrrhinium atropurpureum* Schott recently opened flowers have deep wine-red petals with a normal petal texture, crinkled filaments, and closed anthers; putatively receptive flowers have inflated, very pale lavender petals, stiff filaments, and dehisced anthers; the pale petals provide a dramatic contrast to the rest of the inflorescence, which is a uniform deep wine red, even to the axes, and the petal texture is unlike that of any other flower known to us, aerenchyma-rich, resembling the hollow structure of certain rubiaceous fruits such as *Coccocypselum* (C. Proença, pers. obs.). It seems likely that *Acca* and *Myrrhinium* evolved under selection for bird pollination (perhaps in areas with an impoverished bee fauna) without totally losing their adaptations to bee pollination, so that in cultivation *Acca sellowiana* at least still responds to bee pollination.

MAMMAL POLLINATION

Long-tailed pygmy possums (*Cercartetus caudatus*) feed on *Syzygium cormiflorum* in northern Queensland (Hopper, 1980). Beardsell et al. (1993) suggested that the cauliflorous flowering of several

Syzygium species might facilitate access to the flowers by larger marsupials, which move up and down the trunks and larger branches. These authors also stressed that bats, being nocturnal and not easily studied, might be more significant pollinators of some Myrtaceae than had been thought previously. *Syconycteris australis* (Queensland blossom bat) appeared to be one of the minor pollinators of the night-flowering rainforest tree *Syzygium tierneyanum* (Hopper, 1980) and also made nocturnal visits to the flowers of the cauliflorous *S. cormiflorum* (Crome & Irvine, 1986) as did *Macroglossus lagochilus*, another small blossom bat. In *S. cormiflorum* flowers open at any time of the day or night, but bats were the single most important pollinators, although visits by birds to the flowers were more frequent and more numerous. Start and Marshall (1976) reported the bats *Eonycteris spelaea* and *Macroglossus minimus* feeding on *S. malaccense* in West Malaysia.

WIND POLLINATION

Grifo (1992) considered wind-pollination possible but unlikely in *Myrcianthes*. Peters and Vasquez (1986/87) mentioned the possibility of wind-pollination in *Myrciaria dubia* and Moncur (1988) the same for *Acca sellowiana* (as *Feijoa sellowiana*), but in both of these studies bees were considered to be the most important pollinating agents.

Fruits

FRUIT CHARACTERISTICS AND DISPERSAL AGENTS

The typical fruit of the Myrtoideae is a fleshy single-seeded, usually orange, red, or black berry, and the Myrtoideae have long been characterized as a fleshy-fruited subfamily or tribe. However, semi-dry to dry berries (i.e., leathery or pithy) have also been recorded, especially in *Eugenia* and related genera. Drupaceous fruits are reported for *Myrtella* and *Stereocaryum*. Subdrupaceous fruits, with variable levels of woodiness of the endocarp, are found in some species of *Eugenia* s.l., *Rhodomyrtus* (Schmid, 1980), and in *Acmena* (Hartley & Craven, 1977). Drupoid fruits with 1–3 pyrenes occur in *Eugenia* and *Hexachlamys* (Berg, 1857; Rotman, 1982). A very specialized "drupoid" fruit occurs in *Campomanesia*. It may be considered drupoid in that the single seeds developing in each of the locules adhere to the endocarp, as in a true drupoid fruit, but it differs in the texture of the endocarp, which can be woody or merely glandular-verrucose, simulating a false seed-coat (Landrum, 1982). The more primitive subtribe Myrtinae includes many species that have green or yellow, several- to many-seeded fruits.

Our knowledge of dispersal agents is mainly based on deductions from fruit morphology; few actual dispersal events have been reported. Fleshy perigynia have clearly evolved in association with zoochory. Briggs and Johnson (1979) highlighted two common secondary developments that may occur independently or in conjunction, viz., increase in fruit size and reduction in seed number. Proença (1991) suggested that single-seeded fruits, i.e., "packaging each seed separately," would enable the plant to abort inferior zygotes on an individual basis and to mature fruits at different rates, thus permitting more dispersal events for the same number of seeds.

Various dispersal mechanisms have been suggested for many-seeded fruits. Landrum (1986) considered that most species of *Campomanesia* best fit the mammal dispersed syndrome as defined by Janson (1983) based on an Amazon rainforest community, but Snow (1981) registered *Campomanesia* as forming part of the diet of specialized frugivorous birds. Motta Júnior et al. (1994) reported that *Dusicyon thous*, a small nocturnal Canidae, feeds on fruits of *Psidium* sp., *Campomanesia* sp., and *Plinia cauliflora* (as *Myrciaria cauliflora*). Seeds of *Campomanesia* sp. recovered from scats germinated successfully both *in situ* and in the laboratory, indicating that this small mammal is a potentially effective dispersal agent. The genus *Psidium* is cited by Snow (1981) as having fruits that form part of the diet of specialized frugivorous birds, but *Psidium firmum* is apparently consumed by small rodents (Proença, 1991). Evidence to this effect included a gnawed-through peduncle of an unripe fruit, marks of superficial bites on unripe fruit, ripe fruit torn open and the flesh partly eaten, and nearby scats which were identified as pertaining to *Rhipidomys* or *Oryzomys*. Cultivated *Psidium guajava* is eaten by parrots (M. A. S. Alves, pers. comm.), other birds (Advani, 1981), and bats (Funmilayo, 1980; Advani, 1982). Other multi-seeded fruits mentioned by Snow (1981) include those of *Decaspermum* and *Rhodamnia*, which are exploited by specialized frugivorous birds, and *Calycolpus*, exploited by specialized and unspecialized frugivorous birds. Kevan and Lack (1985) observed mistletoe-birds (Dicaeidae) feeding on the fruits of *Decaspermum parviflorum* and discussed bird dispersal in this dioecious species in relation to the selective pressure for the production of energy-rich fruits. Ant-dispersal by *Messor minor* (André) has recently been reported for *Myrtus communis*, the

seeds of which bear elaiosomes (Aronne & Wilcock, 1994)

Johnson and Briggs (1984) suggested that in diverse lines of Myrtaceae, fruits with large, single seeds seem to be adapted to vertebrate dispersal in tropical forest. In the large genus *Syzygium*, one-seeded fruits are the norm, but mature fruits from different species may differ in diameter by an order of magnitude (Hyland, 1983). K. Fischer (pers. comm.) compared the morphology and nutritional and secondary chemistry of fruits of New Guinean species of *Syzygium* eaten by birds and by bats. In the species of *Syzygium* studied by her, fruits eaten by bats were both longer and wider than those consumed by birds but did not differ in nutrient composition or secondary chemistry. Among 16 wild fruits edible to man that were studied in Malawi, *Syzygium guineense* Guill. & Perry had the highest levels of iron and magnesium (Saka & Msonthi, 1994). Beardsell et al. (1993) noted that in many species of *Syzygium* the infructescences are borne at some distance from the tips of the branches thus allowing larger animals access to the fruits. They cited the extreme case of *Syzygium cormiflorum*, the berries of which develop on the main trunk and larger branches, and suggested that this arrangement enables larger marsupials to eat the fruits during tree to tree movements. Fruits of a cauliflorous species of *Myrciaria* are eaten by bats (Semir, 1984). *Eugenia* s.l. is cited as consumed by unspecialized frugivorous birds (Snow, 1981). Two unidentified species of *Eugenia* s. str. from Costa Rica are eaten by *Pharomachrus mocinno* (Trogonidae) and by *Aulacorhynchus prasinus* (Rhamphastidae), respectively (Wheelwright et al., 1984). Fruits of *Eugenia punicifolia* (Kunth) DC. are probably consumed by pheasant-like Tinamidae in central Brazil, and *Siphoneugena densiflora* fruits are eaten by *Miyarchus swansonii* (Tyrannidae), an opportunistic fly-catcher, and by other birds (Proença, 1990). Fruits of *Myrcia torta* DC. (as *Myrcia dictiophylla*) are eaten by *Neothraups fasciata* (Emberizidae), a generalist low-foraging tanager (Alves, 1992). Observations of *Blepharocalyx salicifolius* revealed that the fruits are swallowed whole by migratory *Elaenia chiriquensis* and *Tyrannus melancholicus* (both Tyraniidae) and by resident *Neothraups fasciata* (Emberizidae), all opportunistic frugivores that also feed on insects (Paes, 1993). Snow (1981) listed *Acmena, Eugenia, Myrcia,* and *Syzygium* as forming part of the diet of specialized frugivorous birds, while fruits of *Eugenia* and *Myrcia* are also exploited by non-specialized birds. He commented that while at least 13 genera of Myrtoideae provide fruits that are eaten by frugivorous birds, specialized and unspecialized, none seems to provide the staple diet of any frugivorous bird. In this respect the Myrtoideae resemble the Euphorbiaceae but differ from the Lauraceae, Burseraceae, and Palmae. Grifo (1992) saw monkeys of the genus *Alouatta* consuming the fruits of *Myrcianthes pungens* in Corrientes, Argentina. However, her observations suggested that the fruits, including the seeds, were chewed, thus considerably reducing the possibility that the monkeys were agents of dispersal.

OVULE-SEED RATIOS AND REPRODUCTIVE CAPACITY

In the fruits of most Myrtoideae, including the many-seeded ones, the number of mature seeds is much smaller than the original number of ovules in the ovary from which the fruit is derived. Even in genera in which the ovule number is reduced to two in each of two (or three) locules, most ovules do not develop into mature seeds. This superfluity of ovules may simply represent a relictual situation, with these species being derived from taxa in which most or all ovules within the ovary would have matured into seeds (Caspar & Wiens, 1981). For example, Landrum (1981) envisaged an ancestor of *Myrceugenia* that developed all or nearly all its ovules into seeds while in present-day species few ovules develop into seeds. Alternatively, the superfluous ovules may provide scope for the exercise of female choice (Stephenson & Bertin, 1983) and/or allow for the wastage of ovules inherent in a postzygotic "self-incompatibility" system. In the dioecious *Pimenta dioica* (and the putatively dioecious *P. guatemalensis*) the number of ovules scarcely exceeds the number of seeds per fruit (Landrum, 1986). We suggest that in these species there is no need for superfluous ovules, since all pollen tubes must originate from non-self pollen.

In the Australian Myrtaceae (largely Leptospermoideae), Rye and James (1992) identified reduction in ovule numbers and competitive selection among fertilized ovules as mechanisms leading to reduction in seed number. These trends were interpreted as the result, in part at least, of selection for larger seed size. In addition, they found that plant size is positively correlated with ovule number and seed set, and that the effects of all these factors tended to reinforce each other in determining the net reproductive capacity of the species.

Another factor that has been linked to reproductive capacity is chromosome number. Rye and James (1992) found that high reproductive capacity is associated with high dysploid chromosome numbers in four genera including *Eugenia*.

Embryo and Seed Development

EMBRYO DEVELOPMENT

The Myrtoideae apparently follow the onagrad pattern of embryo development but, as in the Myrtaceae as a whole, the process has scarcely been studied. The dearth of information in this area is acute, even in the context of our rudimentary knowledge of Myrtoideae biology in general, and may be attributable to the extreme difficulties experienced in fixation for histological studies in the family (Mauritzon, 1939; Davis, 1968; Beardsell et al., 1989, 1993).

SEED-COAT

Beardsell et al. (1993) considered a seed-coat formed from both integuments as "a feature of all Myrtaceae so far examined." While this may summarize the situation in the Leptospermoideae it is far from true with respect to the Myrtoideae. Van Wyk and Botha (1984) reported testa formation from the outer integument only in some southern African *Eugenia* species and a pachychalazal seed-coat in others. Narayanaswami and Roy (1960b) described the testa in *Psidium guajava* (and in *P. cujavillus* Burm. f., now considered synonymous) as being formed from the outer integument only. The seed-coat appears to be entirely absent in *Acmena*, *Acmenosperma*, and *Waterhousea* (Hartley & Craven, 1977; Hyland, 1983).

McVaugh (1968) indicated that the testa varied in thickness from group to group in the neotropical Myrtoideae and may be membranous, leathery, cartilaginous, or bony. Where the seed-coat is hard (i.e., in most Myrtinae apart from Landrum's *Campomanesia* complex), an operculum in the seed-coat, located directly over the basal end of the hypocotyl, allows the embryo to emerge. Landrum and Stevenson (1986) detected a strong correlation between seed-coat texture and embryo structure but admitted the possibility that changes in embryo morphology naturally follow changes in seed-coat texture. Whatever the thickness, the testa is usually quite smooth and unsculptured.

In *Campomanesia* the thick glandular locule wall adheres to the delicate membranous testa of the single seed maturing inside the locule, as described above. The locule wall thus serves as a false seed-coat, to which Landrum (1982) attributed a protective function, hypothesizing that frugivorous birds or mammals would tear apart the fruits without biting into the glandular turpentine-smelling walls. Some field observations support this theory, as partially eaten fruits were found to have the locules intact (Landrum, 1986) but, as discussed above, some seeds are clearly ingested by small mammals (Motta Júnior et al., 1994). Proença (1991) suggested a possible co-adaptive role for the pseudotesta, interpreting it as a defense to prevent developing larvae of Tephritidae flies from migrating from infected to healthy locules. The situation in *Campomanesia*, where each locule harbors a single developing embryo, was compared to that in a species of *Berberis* in which high mortality of Tephritidae larvae was found to occur in single-seeded fruits when compared to several-seeded fruits (Herrera, 1984). Tephritidae are notorious predators of myrtaceous fruit crops (Malavasi & Morgante, 1980; Morgante & Malavasi, 1981; Tan & Lee, 1982; Burk, 1983).

EMBRYO STRUCTURE

Embryo structure has been considered fundamental in the classification of the Myrtoideae since the time of De Candolle (1828). He distinguished three basic embryo types commonly referred to as eugenioid (with thick, fleshy cotyledons and a relatively insignificant hypocotyl), myrcioid (with leafy cotyledons that are much broader than the hypocotyl), and myrtoid/pimentoid (with a well-developed hypocotyl and relatively small, narrow cotyledons). Although most subsequent authors have used these differences as the basis for their classifications, little attention has been paid to the biological significance of these structures. One notable exception is the discussion by Landrum and Stevenson (1986) in which the various embryo types are interpreted as different responses to the same selective pressure for increased food storage in the embryo. Essential oil-secreting schizogenous glands occur in the embryos of *Pimenta racemosa* (P. Miller) J. W. Moore (as *Myrcia acris* DC.), *Luma apiculata* (as *Myrceugenia apiculata*), *Myrceugenia glaucescens* (Cambess.) D. Legrand & Kausel (as *Eugenia glaucescens* Cambess.), *Myrcianthes pungens* (as *Eugenia pungens*), and *Eugenia discolor* DC. and are absent from *Myrtus* sp., *Psidium*, *Acca* (as *Feijoa*), and *Eugenia uniflora* (as *Stenocalyx michelii*) (Petit, 1908). In a study of southern African *Eugenia*, four species had conspicuous glands and five species were described as "apparently eglandular but usually with a few obscure glands mainly associated with the radicular protuberance" (van Wyk, 1980). Hyland (1983) recorded oil glands in the embryos of 4 out of ca. 50 species of Australian *Syzygium* studied, i.e., *S. macilwraithianum* B. Hyland, *S. sayeri* (F. Muell.) B. Hyland, *S. velae* B. Hyland, and *S. wilsonii* B. Hyland. In

the Leptospermoideae the embryo lacks oil glands (Petit, 1908).

ENDOSPERM

The endosperm is nuclear and is generally described as being digested by the developing embryo and therefore absent from the mature seeds (Tobe & Raven, 1983). However, studies by Petit (1908, cited in van Wyk & Botha, 1984) have shown that traces of endosperm are present in many myrtaceous seeds including those of the genera *Acca* (as *Feijoa*), *Myrtus*, and *Psidium* (all Myrtoideae). Van Wyk and Botha (1984) reported the presence of endosperm in mature seeds of some species of southern African *Eugenia*. They suggested that variation in the amount of endosperm formed in the young seed may be of taxonomic importance, whereas the quantity of endosperm that remains in mature seeds is variable within species and therefore less likely to prove taxonomically significant.

POLYEMBRYONY

Tobe and Raven (1983) described polyembryony as usual in *Syzygium* but our literature survey suggests that, though frequent, it is by no means the norm in this genus. The earliest reports are by Tiwary (1926), who concluded that all (six) of the species of *Syzygium* (reported as *Eugenia*) examined by him showed "the existence of some kind of polyembryony." However, as he interpreted early bifurcation of the plumule as evidence of polyembryony, he may have overestimated the frequency of this latter phenomenon within the genus. In only two of the species he examined (*S. cumini* and *S. jambos*, as *Eugenia jambolana* and *E. jambos*, respectively) was the presence of more than one embryo in the seed actually demonstrated.

Subsequent studies have confirmed the existence of polyembryony in *Syzygium jambos*, disputed its occurrence in *S. cumini* (van der Pijl, 1934; Henderson, 1949; Roy, 1953; Chantaranothai & Parnell, 1994) and in general indicated that the condition was far from ubiquitous in the genus. Van der Pijl (1934) reported polyembryony in *S. aqueum* (Burm. f.) Alston (as *Eugenia aquea* Burm.f.), *S. jambos* (as *E. jambos*), *S. javanicum* Miq. (as *E. javanica* Lam.), and *S. malaccense* (as *E. malaccensis*), but found no evidence for polyembryony in *S. cumini* (as *E. cumini*) on the basis of the examination of specimens of this species from four different localities and fruits obtained from the local market. Henderson (1949) found polyembryony in "some species" of the 138 in the genus *Eugenia* s.l. in Malaya, and Merrill and Perry (1938) reported that of the 45 species of *Syzygium* known from China, 5 are regularly polyembryonic (*S. jambos*, *S. buxifolium* Hook. & Arn., *S. megacarpum* (as *S. latilimbum* (Merr.) Merr. & L. M. Perry), *S. forrestii* Merr. & L. M. Perry, and *S. hancei* Merr. & L. M. Perry). Hyland (1983) described ca. 50 species of *Syzygium* occurring in Australia and recorded consistent polyembryony in *Syzygium paniculatum* and the presence of "two-seeded fruits" in *S. aqueum* (polyembryony? see *S. aqueum* above). Chantaranothai and Parnell (1994) found no evidence of polyembryony in *S. cumini*, nor in *S. megacarpum* or *S. formosum*, but confirmed the existence of polyembryony in *S. jambos* and *S. malaccense* and reported production of 2–6 seedlings from 1–3-seeded fruit in *S. siamense* (Craib) P. Chantaranothai & J. Parn. We concur with van Wyk and Botha's (1984) conclusion that most reports of polyembryony in *Eugenia* are probably referrable to the genus *Syzygium*.

Johnson (1936) counted 2–22 embryos in seeds of *Luma apiculata* (as *Eugenia hookeri* Steud.). However, Landrum (1986) revised *Luma apiculata* and, although he had obviously dissected seeds and examined embryos, did not mention the occurrence of polyembryony. Thus we may infer that polyembryony is not constant in this species.

Gurgel and Soubihe Sobrinho's (1951) study of myrtaceous fruit-bearing trees in Brazil is one of the most complete studies of polyembryony in the Myrtoideae to date. Sixteen species were investigated, representing five genera native to Brazil plus *Syzygium*, which is introduced and widely cultivated. The following species were found to be consistently monoembryonic: *Campomanesia* sp. (as *Myrtus mucronata* Cambess.), *Psidium guajava*, *Psidium guineense* (as *Psidium araça* Raddi), *Eugenia uniflora*, *Eugenia tomentosa* Cambess., *Eugenia uvalha* Cambess., *Eugenia myrcianthes* (as *Myrcianthes edulis* O. Berg), *Eugenia brasiliensis* Lam., *Eugenia lucescens* Nied. (as *Phyllocalyx luschnathianus* O. Berg), and *Gomidesia reticulata* O. Berg.

Gurgel and Soubihe Sobrinho (1951) found a high percentage of polyembryony in *Syzygium malaccensis* (66–97%) and *Syzygium cumini* (76–95%). One to eleven embryos were reported per seed. Repeated sampling of these species in successive years suggested the existence of a phenetic as well as a genetic component to the level of polyembryony. A low to medium percentage of polyembryony (33–70%), with one to five embryos reported per seed, was found in the following native Brazilian species: *Plinia cauliflora* (as *Myrciaria cauliflora*), *Plinia trunciflora* (O. Berg) Kausel (as

Myrciaria trunciflora O. Berg), and *Plinia edulis* (Vell.) Sobral (as *Eugenia edulis* Vell.), as well as a species cited as *Myrciaria trunciflora*, which Mattos (1989), based on the common name, claimed to be *Myrciaria coronata* Mattos. Sobral (1993) excluded this species from *Myrciaria* in his recent revision of that genus and stated that it is a *Plinia*. Rotman (1982) registered consistent polyembryony in *Guapurium peruvianum* (possibly = *Plinia*) but registered no polyembryony in *Plinia trunciflora*. Thus all low to medium polyembryonic species may be members of genus *Plinia*. Traub (1939) had already noted that polyembryony was usual in *Plinia cauliflora* (as *Myrciaria cauliflora*) cultivated in Florida.

Observations on the origin of the embryos in polyembryonic seeds are few and disparate. Tiwary (1926) reported embryos originating from the egg cell (presumbly sexual), from the synergids and from the nucellus in *S. cumini* (as *Eugenia jambolana*). Narayanaswami and Roy (1960a) and Roy and Sahai (1962) also studied *S. cumini*, and the latter authors found that the fertilized egg degenerates along with the synergids. The upper half of the nucellus becomes proliferative and produces several embryos, one or more of which may survive, producing mono- or polyembryonic seeds in this species. Roy and Sahai (1962) also noted the occasional production of supernumerary embryo-sacs (by apospory or by the activity of more than one archesporial cell) but reported that ovules in which this occurs eventually degenerate. The multiple embryos in seeds of *S. jambos* are also of nucellar origin (van der Pijl, 1934), and Johnson (1936) tentatively suggested a nucellar origin for the embryos of *Luma apiculata* (as *Eugenia hookeri*). Gurgel and Soubihe Sobrinho (1951) confirmed that in *S. jambos* the sexual embryo often dies immediately after fertilization. However, they considered the adventitious embryos to be derived from the inner integument. Van der Pijl (1934) reported an integumentary origin for the multiple embryos of *Syzygium malaccense* (as *E. malaccensis*).

REGENERATION FROM SEED

Beardsell et al. (1993) highlighted the lack of published data on the regeneration of the Myrtoideae of the tropical forests. They suggested that germination requires breakdown of the pericarp by weathering or ingestion by animals including birds, and reported that some species of *Syzygium* germinate after fermentation of the fruits. Tidbury (1949) also advocated fermentation of fruits. When fruits of *Syzygium aromaticum* (Clove Tree) were left to ferment for about three days the seeds were easily hulled, and such hulled seed produced "somewhat better seedlings" than unhulled. Germination was rapid, occurring within 12–14 days of sowing, and germination percentages were high, almost always above 90%. Hyland (1983) included seedling germination periods in his descriptions of some 50 Australian species of *Syzygium*. Germination periods ranged from 10 days to almost 10 months (300 days) and there was considerable within-species variation in germination time. In the same paper, species of *Acmena* were cited as having even longer germination times, ranging from 24 days to well over 2 years (860 days), while values for *Waterhousea* tended to be lower at 10–60 days. *Eugenia reinwardtiana* (Bl.) DC. and *Acmenosperma claviflorum* (Roxb.) E. Kausel were reported as having germination periods of 30–50 and 40–90 days respectively.

Ferreira (1982) studied germination of seeds of *Psidium acutangulum*, which had been treated with a 1% solution of a proprietary systemic fungicide after being removed from the fruit pulp. He found that germination occurred 30–100 days after sowing and that ca. 90% of seeds planted in loam (the most successful medium) germinated eventually. Lorenzi (1992) reported a similar range of germination times among 16 native Brazilian species (in eight genera) of Myrtaceae studied by him. The most rapid germination (10 days after sowing) was observed in *Eugenia pyriformis* Cambess., while some seeds of *Plinia edulis* (as *Marlierea edulis*) took up to 100 days to germinate. Gurgel and Soubihe Sobrinho (1951) reported germination times between 18 days (for *Psidium guajava*) and 73 days (for *Campomanesia* sp. as *Myrtus mucronata*). Levels of germination varied considerably (40–80%).

Lorenzi (1992) also reported seed viability periods. These were generally short (as little as 2 weeks in *Eugenia involucrata* DC.), but species of *Psidium* and *Acca* had longer seed viabilities of several months. Viability of seeds of *Psidium guajava* may exceed one year. *Blepharocalyx salicifolius* seeds lost viability within two months (Matos, 1994).

CONCLUSIONS

As might be predicted from their morphology, the Myrtoideae emerge from this review as a rather uniform group with respect to their overall pollination and dispersal syndromes. Most species diverge little from the apparently highly successful combination of small, short-lived flowers offering pollen to attract bees as pollinators and fleshy fruits adapted to endozoochory. However, it is possible to ob-

serve that more morphological diversification has arisen in characters linked to seed dispersal and seedling establishment than in those linked to pollination biology. For such a large group, the species exhibit an impressive uniformity with respect to general flower structure and pollen morphology.

The rather narrow pollination spectrum is reminiscent of other large groups with faithful bee pollination, e.g., Malpighiaceae (Anderson, 1979), Melastomataceae (Renner, 1989), and Solanaceae (Symon, 1979). Renner (1989) has suggested that such a lack of diversification may be the result of being "stuck on an adaptive peak." However, the data available suggest that the Myrtoideae run the gamut of flower-visiting bee taxa and fully exploit differences in bee behavior, such as buzzing abilities and trap-lining, the more highly evolved Apidae bee family being dominant. This is reflected in the considerable diversity in flower size, flowering phenology, and especially flowering strategies encountered. The breeding systems of the Myrtoideae vary from dioecy and complete self-sterility (with late-acting variants) through to self-compatibility and apomixis, suggesting that the Myrtoideae have successfully capitalized upon their bee pollinators, and diversified their reproductive strategies accordingly, to establish themselves as important elements in many different life-zones and habitats. In this respect, the Myrtoideae are similar to the Leptospermoideae, although this latter group has coevolved primarily with the most primitive flower-visiting bee family, the Colletidae, while simultaneously developing a secondary evolutionary line of bird pollination, which is very rare in the Myrtoideae. Certain specialized features of the floral biology of the Leptospermoideae are absent in the Myrtoideae, e.g., secondary pollen presentation, wet stigmas, and the presence of ovulodes in the ovary. Conversely, buzz pollination is, as far as we know, limited to the Myrtoideae. Within the Myrtoideae s.l. nectar-rewarding bird pollination systems, postanthesis stylar extension, unitegmic ovules, and apomixis have only been registered in *Syzygium* (of the *Acmena* alliance) and may be restricted to this group (although the possibility of polyembryonic *Plinia* of the Myrtoideae s. str. also being apomictic cannot be discarded as yet).

The endozoochorous fruits of the Myrtoideae seem to be adapted to many different classes of dispersers, and this characteristic is probably the most important ecological difference as compared to the largely wind-dispersed Leptospermoideae. The Myrtoideae show a great variety in size, color, texture, and seediness of fruits, with the seeds also varying significantly in size, seed coat structure, and embryo morphology. Pseudo-testa formation from the endocarp, testa formation from the outer integument only, oil glands in the embryo, and polyembryony are apparently restricted to the Myrtoideae.

Our knowledge of the reproductive biology of the Myrtoideae is still far from complete, and the following questions merit further investigation: Are inflorescence structure and flowering strategy correlated with habitat? Is flowering cued by abrupt fluctuations in humidity? How common is buzz pollination, and what are the adaptations and bees involved? Which birds are involved with bird pollination systems where petals are offered as a reward, why has this mechanism evolved, and how does it differ from nectar-rewarding bird pollination systems? How common is cryptic dioecy and what are the selective pressures maintaining this apparently expensive breeding system? What are the main agents of fruit dispersal and, in particular, how important is the role played by bats and other small mammals? Has co-evolution with parasites affected fruit and seed morphology? What is the nature of the mechanism which maintains preferential outcrossing and does more than one type of self-incompatibility exist in the family? Is there any relationship between apomixis, polyembryony, and chromosome number? The answers to such questions as these may have important and diverse implications. First, they may help to resolve some of the complex taxonomic problems in the Myrtoideae by helping to elucidate the functional significance of characters of taxonomic importance. Second, studies of breeding systems in particular should aid systematists, population geneticists, and ecologists in the interpretation of patterns of variation within and between populations and species. Third, this information may facilitate the genetic improvement of the several economically important species. Finally, a deeper understanding of the reproductive biology of a group that is of great ecological importance in several endangered tropical ecosystems may represent an invaluable contribution toward their conservation.

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THE PHYLOGENETIC UTILITY OF LEMMATAL MICROMORPHOLOGY IN *LEPTOCHLOA* S.L. AND RELATED GENERA IN SUBTRIBE ELEUSININAE (POACEAE, CHLORIDOIDEAE, ERAGROSTIDEAE)[1]

Neil Snow[2]

ABSTRACT

Micromorphological features of the lemma were investigated in the subtribe Eleusininae (Poaceae) using scanning electron microscopy. Ninety-two taxa were studied, which included 48 genera and all currently recognized species of *Leptochloa* s.l. All species of *Leptochloa* and a majority of genera in Eleusininae have cork cells, but silica cells are mostly absent in *Leptochloa* and most related genera in Eleusininae. Enneapogonoid-type microhairs are reported for *Cladoraphis cyperoides* and *Psammagrostis wiseana*, representing only the second report in Eleusininae. Although bicellular microhairs occur in most taxa, variations in microhair type, coupled with the occurrence of partitioning membranes, give them supra-specific phylogenetic utility. The occurrence of papillae on short and long cells varies within *Leptochloa* and between genera. Prickles are ubiquitous in *Leptochloa* and most related genera. Macrohairs are present in all species of *Leptochloa* but absent in some related genera. Clavicorniculate macrohairs are reported for one species each of *Leptochloa* and *Coelachyrum*, and a corniculate macrohair was observed in *Cynodon*. A crispate macrohair occurring in three species of *Coelachyrum* is described for the first time and probably represents a synapomorphy in that genus. The analysis of *Leptochloa* suggests that micromorphological characters vary little within a genus, and thus have the potential to serve as phylogenetic markers at the generic level. Uncertainty concerning the homologous relationships of papillae, hooks, prickles, and macrohairs is discussed in light of this study and previous literature.

RESUMEN

Las características micromorfológicas de la lema en la subtribu Eleusininae (Poaceae) se examinaron utilizando microscopía electrónica de barrido. Se estudiaron 92 taxa, 48 géneros, y todas las especies de *Leptochloa* hasta ahora reconocidas. Todas las especies de *Leptochloa* y la mayoría de los géneros de Eleusininae tienen células suberificadas, pero las células silicífferas están ausentes en *Leptochloa* y en la mayoría de los taxa de Eleusininae. Se reporta por segunda vez en Eleusininae la presencia de micropelos bicelulares de tipo enneapogonoid para *Cladoraphis cyperoides* y *Psammagrostis wiseana*. Aunque los micropelos bicelulares se presentan en casi todos los taxa, variaciones en el tipo de micropelo, junto con la presencia de membranas divisorias les dan valor diagnóstico para estudios filogenéticos supraespecíficos. La presencia de papilas de células cortas y estrechas es variable en *Leptochloa* y entre los otros géneros. Los aguijones se encuentran en todas las especies de *Leptochloa* y la mayoría de los géneros relacionados. Los macropelos están generalmente presentes en todas las especies de *Leptochloa* pero están ausentes en algunos taxa relacionados. Se reportan macropelos clavicorniculados para un especie de ambos géneros *Leptochloa* y *Coelachyrum*, y un macropelo corniculado se reporta para *Cynodon*. Un macropelo crispado en tres especies de *Coelachyrum* es descrito por primera vez, y quizá represente una sinapomorfía de cierto nivel en ese género. El análisis de *Leptochloa* indica que las características micromorfológicas varían poco, y por tanto tienen valor para estudios filogenéticos supraespecíficos. La dificultad sobre las relaciones homólogas de papilas, ganchos, aguijones, y macrotricomas se discute con base a lo hallado en este estudio y con datos anteriores de la literatura.

Cladistic estimations of phylogenetic history with morphological characters tend to favor the use of distinct qualitative characters, or those possessing easily defined character states. This tendency may reflect the potential pitfalls discussed by Chappill (1989) and Stevens (1991) in the uncritical use of

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quantitative characters (but see Thiele, 1993). Used alone, and due to the perception of high levels of homoplasy, characters of gross morphology have been considered inadequate as phylogenetic markers in the grass family (Thomasson, 1978; Hilu & Wright, 1982; Kellogg & Campbell, 1987; Davis & Soreng, 1993; Clark et al., 1995). Not surprisingly, revisionary studies of grasses are turning to micromorphological characters for additional phylogenetic data.

Epidermal micromorphological characters of grasses have systematic value between the ranks of subfamily and species (Prat, 1932; Tateoka et al., 1959; Metcalfe, 1960; Ellis, 1979). Descriptive studies of micromorphological features in grasses have focused on the surfaces of the leaf (Prat, 1932; summary in Ellis, 1976; see also Morden & Hatch, 1987; Dávila & Clark, 1990; Peterson & Annable, 1990; Barker, 1993; Scholz, 1993; Chen et al., 1993), glumes (Lucas, 1979; Molina, 1993), the lemma (Hsu, 1965; Thomasson, 1986; Peterson, 1989; Soderstrom & Zuloaga, 1989; Kellogg, 1990; Zuloaga & Judziewicz, 1991; Valdés-Reyna & Hatch, 1991; Naredo et al., 1993; Ball et al., 1993), and palea (summary in Consaul & Aiken, 1993: 1651). The phylogenetic application of micromorphological characters has been more limited (Peterson & Annable, 1992; Barker, 1993; Visser & Spies, 1994; Guala, 1995).

An Overview of Micromorphological Characters

Several categories of micromorphological characters have been recognized. Short cells (which include cork cells and silica cells), long cells, bicellular microhairs, papillae, hooks, prickles, and macrohairs are all examples of micromorphological characters (Metcalfe, 1960; Ellis, 1979). (See Ellis, 1979, for a summary of alternative terms for hooks and prickles.)

Short cells and long cells are readily distinguished on the basis of relative size, and (when both are present) may constitute a synapomorphy uniting Joinvilleaceae and Poaceae (see also Doyle et al., 1992; Kellogg & Linder, 1995). The differences between short cells and long cells have been documented thoroughly (Kaufman et al., 1969; Kaufman et al., 1970) and are evident in grass fossils of Miocene age (Thomasson, 1978, 1984). The elongation of long cells follows the initial differentiation of long cells and short cells (Kaufman et al., 1969; Kaufman et al., 1970). In addition to their extended length, long cells (unlike short cells) frequently have sinuous margins (Metcalfe, 1960; Clifford & Watson, 1977; Ellis, 1979; Chen et al., 1993). However, the distinction between long and short cells is not always absolute. Thomasson (1978: fig. 1d) illustrated long cells, identifiable by the sinuous margins, having similar dimensions to short cells for a fossilized species of the genus *Nassella* (tribe Stipeae). The two types of short cells recognized are cork cells (sometimes called suberin cells), which accumulate suberin (Kaufman et al., 1970), and silica cells, which accumulate silica into readily observed silica bodies.

Microhairs are bicellular structures that require high magnification for detection (Tateoka et al., 1959). (For exceptions to the bicellular condition see Dahlgren et al., 1985; Renvoize, 1985; and Zuloaga et al., 1989.) They are present throughout the family except in subfamily Pooideae (Johnston & Watson, 1976). Microhairs have been classified as "chloridoid," "panicoid," or "enneapogonoid," based on typological variants (Tateoka et al., 1959; Amarasinghe & Watson, 1988; Watson & Dallwitz, 1992). Only rarely is their ontological status as a distinct character uncertain. For example, as discussed by Barker (1993), the "long slender papillae" (Clayton & Renvoize, 1986: 165) common to several genera in Arundinoideae, given that they are reported to occasionally have the remains of a small apical cell (Renvoize, 1986: 328), may be interpretable as microhairs.

Papillae are short, undifferentiated processes that arise from the outer cell wall.

Hooks have been considered processes having a rounded base and an apex that is at least slightly pointed (Ellis, 1979), but are not recognized as a category in this study (see Discussion). Prickles are basally swollen processes having short, sharp apices that typically point toward the apex of the structure (leaves, glumes, lemmas, or paleas).

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Macrohairs are generally unicellular structures (but see Kabuye & Wood, 1969) visible to the naked eye.

Among lemmatal micromorphological structures, only microhairs have not been reported to accumulate silica. The presence of silica has been reported for cork cells (Kaufman et al., 1972); long cells (Ball et al., 1993); papillae (Terrell & Wergin, 1981; Consaul & Aiken, 1993); prickles (Soni et al., 1970; Kaufman et al., 1972 (as "trichomes"); Terrell & Wergin, 1981; Valdés-Reyna & Hatch, 1991; Ball et al., 1993); and macrohairs (Consaul & Aiken, 1993). (Stomata occasionally occur on lemmas. They are sufficiently infrequent in the taxa examined thus far to be considered an abnormal constituent of the lemma. In a study of the leaf of *Avena*, Kaufman et al. (1972) were unable to find silica in stomatal cells.)

Overview of Lemma Micromorphology

The lemma is the lower of two bracts that (usually) subtend each flower in grasses. The upper bract (the palea) is not homologous to the lemma (Clifford, 1987). The lemma is a transformational serial homology (de Pinna, 1991) of the leaf by virtue of its "ontogenetic individualization" (sensu Wagner, 1989a, b) from the leaf (Philipson, 1934; Tran, 1973; Kellogg, 1990). Its transformational derivation from the leaf is supported by rare atavisms in mutants to a leaflike progenitor having sheath, ligule, and blade (Philipson, 1934), its diminuitive size relative to regular leaves, its restricted occurrence in the inflorescence, the occasional presence of lemmatal stomata (common to the leaf), and the frequent infraspecific differences of micromorphological features between the leaf and lemma (Thomasson, 1978: 977; Terrell & Wergin, 1981: 706; Snow, unpublished).

The most extensive work on lemma micromorphology in Eleusininae was that of Valdés-Reyna and Hatch (1991). Their survey in Eragrostideae of 57 species (representing 30 genera) suggested such characters might be useful phylogenetic markers in the subtribe Eleusininae. This study extended their generic survey of micromorphology (Valdés-Reyna & Hatch, 1991) to include genera of Eleusininae not previously examined, including a few other genera in Chloridoideae, and to characterize these features for all species in *Leptochloa*.

An Overview of the Systematics of Chloridoideae

The grasses are composed of at least four monophyletic subfamilies and contain a number of tribes with uncertain phylogenetic affinity (Dahlgren et al., 1985; Kellogg & Campbell, 1987; Doyle et al., 1992; Davis & Soreng, 1993; Barker et al., 1995; Clark et al., 1995; Kellogg & Linder, 1995). The subfamily Chloridoideae Rouy has about 1300 species, which tend to occupy dry, warmer climates (Hartley & Slater, 1960). (Taxonomic concepts follow Clayton & Renvoize, 1986.) The largest tribe, Eragrostideae Stapf, has about 80 genera and 1000 species. Within Eragrostideae, the most diverse subtribe is Eleusininae Dumort, and only the highest latitudes are excluded from the overall range of its approximately 55 genera. Relatively few genera in Eleusininae occur outside of a single continent (e.g., *Coelachyrum, Eragrostis, Leptochloa, Trichoneura,* disregarding minor exceptions and a few cosmopolitan weeds). Excluding *Eragrostis,* with its approximately 350 species (Clayton & Renvoize, 1986; Van den Borre & Watson, 1994), most of the approximately 600 species in the subtribe occur in relatively small genera (10 species or fewer). *Leptochloa* P. Beauv. is a nearly worldwide genus of about 35 species, although many continue to segregate the genus *Diplachne* (McNeill, 1979; Phillips, 1982; Watson & Dallwitz, 1992; Simon, 1993; Nicora, 1995).

Recent intergeneric studies in Eleusininae differed in the taxa, characters, and analytical methodologies, which hampers meaningful comparisons between the results (Phillips, 1982; Hilu & Wright, 1982; Campbell, 1985; Hilu & Esen, 1993; Duvall et al., 1994). The position of *Leptochloa* in the generic arrangement of Clayton and Renvoize (1986: 192) suggests three non-mutually exclusive possibilities: (1) that *Leptochloa* has many close generic relatives, (2) that *Leptochloa* is evolutionarily basal to related genera, and (3) that *Leptochloa* may be paraphyletic as currently recognized. The monophyly of most chloridoid groups, including *Leptochloa,* remains largely untested.

The purpose of this paper is to create a more extensive data set for inferring phylogenetic relationships in *Leptochloa* and Chloridoideae (Snow, in prep.). In addition, terminological inconsistencies throughout the literature, coupled with the results herein, provide a basis to question the ontological status of several characters, and suggest the need for a critical reevaluation of the characters.

Material and Methods

The adaxial surface of the lemma was studied for 92 taxa using scanning electron microscopy (SEM) at the Electron Microscopy Laboratory at Washington University (Appendix 1). Samples were re-

moved directly from herbarium specimens. To assure the use of semaphorants (Wiley, 1981: 119), I generally sampled lemmas from spikelets that contained mature caryopses. This precaution was important, because spikelets in early stages of ontogeny may be present even when the inflorescence is well exserted from the leaf sheath. Three specimens of most taxa were observed. Some samples were sonicated in xylene for 30 minutes to remove the epicuticular waxes that can obscure surface features, but this treatment was not always effective. After being placed on aluminum stubs the specimens were coated with gold using a Polaron E5000 sputter coater. Samples were observed with 0° tilt at 20 kV on a Hitachi S-450 SEM and photographed using Polaroid 55 positive-negative film. Except for Figures 10 and 42, all photomicrographs have the apex of the lemma directed toward the right. Attempts to standardize the scale of photomicrographs proved unworkable, since various magnifications were necessary.

The format differs from Valdés-Reyna and Hatch (1991) in that microhairs and macrohairs are included, my interpretation of papillae on short cells is different (see Results), and the degree of undulation of the long cells with papillae was not recorded. Valdés-Reyna and Hatch (1991) discussed their findings based on four variations of cork cell occurrence: cork cells adjacent to silica cells; cork cells not adjacent to silica cells; cork cells papillate; or cork cells not observed. This study merely recorded cork cells as a binary character (present or absent). I will refer to taxa in Eleusininae besides *Leptochloa* as "Other Eleusininae Taxa" (OET), whereas other taxa in Eragrostideae (fide Clayton & Renvoize, 1986) will be designated "Other Eragrostoid Genera" (OERG).

This study focused on the presence or absence of characters. No attempt was made to measure quantitative variation of the characters, but distribution and frequency on the lemma is sometimes discussed.

Results

A summary of lemmatal microcharacters observed is presented in Table 1. For comparison, the results of Valdés-Reyna and Hatch (1991) are intercalated therein. Unless noted otherwise these results accord with those of Valdés-Reyna and Hatch (1991) for taxa examined in both studies. Figures are presented at the end of the text, arranged in alphabetical order by genus name. Figures are not presented for all taxa and characters observed or discussed, but virtually every character recorded (except those with question marks, Table 1) was verified with a photomicrograph.

Cork cells. Cork cells were abundant in the intercostal zones in all species of *Leptochloa,* and alternated with long cells. As was true of all micromorphological characters studied, their distribution could vary significantly on a single lemma. There was a general tendency for cork cells to decrease in frequency near the apex.

Among OET, cork cells were absent in *Desmostachya* (Fig. 14), *Ectrosia gulliveri* (Fig. 17), *Ectrosiopsis, Odyssea mucronata* (Fig. 60), and *Psammagrostis* (Fig. 65). Unlike its congener, *Odyssea paucinervis* has cork cells. The cork cells of *Apochiton* (Fig. 2), *Halopyrum* (Fig. 23), and *Neyraudia* (Fig. 58) were not noticeably darkened, as is common for mature cork cells under SEM observation (Valdés-Reyna & Hatch, 1991). However, since their size and location suggested cork cells, they were recorded as present (Table 1).

Cork cells were present in all OERG except *Spartina* (not shown). With the exception of a sparse distribution in *Tragus* (not shown), cork cells were common in OERG.

Some taxa had short cells resembling cork cells in size, and from which other structures could be seen developing, such as bicellular microhairs (e.g., *Bewsia,* Fig. 3), prickles (e.g., *Diplachne gigantea,* Fig. 38, *Leptochloa rupestris,* Fig. 48), and macrohairs (e.g., *Leptochloa fascicularis,* Fig. 36, *L. neesii,* Fig. 45). Many taxa such as *Eragrostiella* (Fig. 20) and *Indopoa* (Fig. 26) had short cells whose outer walls were rounded in profile, and which were ontogenetically destined to become cork cells. (Valdés-Reyna & Hatch (1991: 536) referred to these as papillate cork cells.) That they were destined to become cork cells became evident by examining different stages of development on a lemma, in which cells at the apical and basal portions were in different stages of development. The initially rounded outer walls of short cells appear to collapse coincident with or prior to suberin deposition; this process was evident in the shrunken tissue of the outer wall, coupled with darkened lumens of the short cells (e.g., *Leptocarydion,* Fig. 28, *Leptochloa uniflora,* Fig. 51, and *L. virgata,* Fig. 52).

Silica cells. Silica cells were absent in all species of *Leptochloa* except for *L. monticola* (Fig. 41), which had abundant silica cells in all specimens examined, and one specimen (*Snow 5811-A*) of *L. fascicularis* (Fig. 35), which had a few silica cells present in the intercostal regions.

A majority of OET genera had silica cells. In *Halopyrum* (Fig. 23, not visible) they were poorly developed (minimal silica deposition?), obscured

Table 1. Summary of lemmatal micromorphological characters for species of *Leptochloa*, most genera in Eleusininae, and a few genera in Eragrostideae outside Eleusininae (fide Clayton & Renvoize, 1986). Genera not included in Eleusininae are indicated with a double asterisk. Taxa are arranged alphabetically. Taxa examined by Valdés-Reyna and Hatch (1991) but not examined herein are followed by single asterisk; their data are intercalated for convenience by: (1) relying on Watson and Dallwitz (1992) for the type of microhair (as they determined from leaf blades); (2) examining herbarium material for the presence of prickles and macrohairs (Appendix 1); and (3) by leaving a question mark in the column for papillate short cells, since their interpretation of papillae differed (see Results). The generic abbreviation for species tentatively placed in *Leptochloa* that apparently lack a valid combination in the latter is *D.* (for *Diplachne*) + specific epithet. Abbreviations: + = present; − = absent; BM = bicellular microhairs (C = chloridoid, P = panicoid, E = enneapogonoid); Macrohairs (N = normal, CC = clavicorniculate, A = apiculate, CR = crispate); PLC = papillate long cells; PSC = papillate short cells.

Taxon	Cork	Silica	BM	PLC	PSC	Prickles	Macrohairs
Acrachne racemosa	+	−	C	−	−	+	−
Apochiton burttii	+	−	C	−	−	+	N
Bewsia biflora	+	−	C	−	−	+	N
*Bouteloua curtipendula***	+	−	C	−	−	+	N
Brachychloa schiemanniana	+	−	C	−	−	+	−
*Chloris paniculata***	+	−	C	−	−	+	N
*Chloris verticillata***	+	−	C	−	−	+	N
Cladoraphis cyperoides	+	+	E	−	−	+	N
Cladoraphis spinosa	+	+	−	−	−	+	−
Coelachyrum brevifolium	+	−	C	−	−	+	CR
Coelachyrum poiflorum	+	−	C	−	−	+	CR
Coelachyrum stoloniferum	+	−	C	−	−	+	CR
Coelachyrum yemenicum	+	−	C	−	−	+	CC
*Chondrosum gracile***	+	−	C	−	−	+	N
*Cynodon nlemfuensis***	+	−	C	−	−	+	A/N
*Dactyloctenium**	+	−	C	−	?	−	−
Desmostachya bipinnata	−	+	C/P	−	−	+	−
Dinebra polycarpha	+	−	C	+	+	+	N
Dinebra retroflexa	+	−	C	+	+	+	N
Drake-Brockmania haareri	+	−	C	+	+	+	N
Drake-Brockmania somalensis	+	−	C	+	+	+	N
Ectrosia gulliveri	−	+	P	−	−	+	N
Ectrosia leporina	+	+	P	−	−	+	−
Ectrosiopsis lasioclada	−	+	P	−	−	+	−
Eleusine indica	+	+	C	−	−	+	−
Eragrostiella bifaria	+	−	C	−	−	−	−
Eragrostis spp. *	+	+	C/P	−	?	+	−
Erioneuron spp.*	+	+	C	−	?	+	N
Gouinia virgata	+	−	C	−	−	+	N
Habrochloa bullockii	+	−	P	−	−	+	N
Halopyrum mucronatum	+	+	C	+	+	+	N
Harpachne schimperi	+	+	C	−	−	+	±
Heterachne abortiva	+	+	P	−	−	+	−
Indopoa paupercula	+	−	C	−	−	+	N
Kengia serotina	+	+	C	+	−	+	N
Leptocarydion vulpiastrum	+	+	C	−	−	+	N
Leptochloa aquatica	+	−	C	−	−	+	N
D. caudata	+	−	C	−	−	+	N
Leptochloa chinensis	+	−	C	+	−	+	N
Leptochloa chloridiformis	+	−	C	−	−	+	N
Leptochloa ciliolata	+	−	−	−	−	+	N
Leptochloa coerulescens	+	−	C	+	−	+	N
D. cuspidata	+	−	−	+	−	+	N
Leptochloa decipiens	+	−	−	−	−	+	N
Leptochloa digitata	+	−	C	−	−	+	N
Leptochloa divaricatissima	+	−	C	−	−	+	N

Table 1. Continued.

Taxon	Cork	Silica	BM	PLC	PSC	Prickles	Macrohairs
Leptochloa dubia	+	−	C	−	−	+	N
D. eleusine	+	−	C	−	−	+	CC
Leptochloa fascicularis	+	±	C	+	+	+	N
Leptochloa fusca	+	−	C	+	+	+	N
D. gigantea	+	−	C	+	+	+	N/−
Leptochloa ligulata	+	−	C	−	−	+	N
Leptochloa longa	+	−	C	−	−	+	N
Leptochloa marquisensis	+	−	C	−	−	+	N
Leptochloa monticola	+	+	C	−	−	+	N
Leptochloa mucronata	+	−	C	−	−	+	N
D. muelleri	+	−	C	+	+	+	N
Leptochloa nealleyi	+	−	C	−	−	+	N
Leptochloa neesii	+	−	C	−	−	+	N
Leptochloa obtusiflora	+	−	C	−	−	+	N
Leptochloa panicea	+	−	C	+	−	+	N
Leptochloa panicoides	+	−	C	+	+	+	N
D. parviflora	+	−	C	+	−	+	N
Leptochloa rupestris	+	−	C	−	−	+	N
Leptochloa scabra	+	−	C	−	−	+	N
Leptochloa sp. nov. (Snow, in prep.)	+	−	C	−	−	+	N
Leptochloa squarrosa	+	−	C	+	−	+	N
Leptochloa uniflora	+	−	C	−	−	+	N
Leptochloa uninervia	+	−	C	+	+	+	N
Leptochloa virgata	+	−	C	−	−	+	N
Leptochloa viscida	+	−	C	+	+	+	N
Leptochloa xerophila	+	−	C	−	−	+	N
*Lintonia nutans***	+	−	C	−	−	+	N
Lophacme digitata	+	−	C/P	−	−	+	N
*Munroa squarrosa**	−	−	C	+	?	+	N
Myriostachya wightiana	+	+	C	−	−	+	−
Neesiochloa barbata	+	−	C	−	−	+	N
Neyraudia reynauldiana	+	−	P	−	−	+	N
Ochthochloa compressa	+	−	C	−	−	+	N
Odyssea mucronata	−	+	C	+	−	+	N
Odyssea paucinervis	+	+	C	+	−	+	N
Orinus thoroldii	+	−	C	+	+	+	N
Oropetium aristatum	−	−	C	+	−	+	N
Pogonarthria fleckii	+	+	C	−	−	+	N
Pogoneura biflora	+	+	C	−	−	+	N
Psammagrostis wiseana	−	+	E	−	−	+	−
Psilolemma jaegeri	+	+	C	−	−	−	−
*Redfieldia flexuosa**	−	−	C	−	?	+	−
Richardsiella eruciformis	+	+	C	−	−	+	N
Sclerodactylon macrostachyum	+	+	C	−	−	+	−
*Scleropogon brevifolius**	+	+	C	+	?	+	N
*Sohnsia filifolia**	+	+	C	−	?	−	−
*Spartina pectinata***	−	+	C	−	−	+	N
Steirachne barbata	+	+	C	−	−	+	−
*Tragus pedunculatus***	+	+	C	+	+	+	N
Trichoneura grandiglumis	+	−	C	−	−	+	N
Tridens spp.*	+	−	C	−	?	+	N
Triplasis spp.*	+	−	C	−	?	±	N
Tripogon major	+	−	C	−	−	+	N
Triraphis andropogonoides	+	+	P	−	−	+	N
*Vaseyochloa multinervosa**	+	−	C	−	?	+	N
Viguierella madagascariensis	+	+	−	−	−	+	−

by epicuticular waxes, or both. *Kengia* (Fig. 27, not visible) and *Eleusine* (not illustrated) had a few silica cells that were localized over the costal zones. The proximity of silica cells to cork cells was a character noted by Valdés-Reyna and Hatch (1991). Silica cells were not adjacent to cork cells in *Desmostachya* (Fig. 14), *Ectrosia gulliveri* (Fig. 17), *Ectrosiopsis* (Fig. 19), *Myriostachya* (Fig. 56), *Odyssea mucronata* (Fig. 60), and *Steirachne* (Fig. 69). Silica cells were adjacent to cork cells in *Cladoraphis* (Fig. 7), *Ectrosia leporina* (Fig. 18), *Harpachne* (Fig. 24), *Odyssea paucinervis* (not shown), *Psilolemma* (Fig. 66), *Richardsiella* (Fig. 67), and *Sclerodactylon* (Fig. 68). In *Pogonarthria* (Fig. 63) and *Triraphis* (Fig. 71) their location varied (cork cells adjacent to silica cells not shown for *Triraphis*). It was uncertain whether the dark, narrow bands adjacent to some silica cells in *Heterachne* (Fig. 25) were artifacts of preparation (e.g., shrinking of cell walls adjacent to the silica bodies noted by Kaufman et al., 1972: fig. 6, and Terrell & Wergin, 1981) or whether the narrow bands were cork cells that were partially obscured by overarching silica bodies; the uncertainty was enhanced because not all silica cells had adjacent bands. Since a few short cells with dark lumina were visible adjacent to some silica cells, cork cells were scored as present for *Heterachne*. I did not observe silica cells on *Leptocarydion*, but given their observation by Valdés-Reyna and Hatch (1991: fig. 24, tab. 2), they were recorded as present (Table 1).

Among OERG, silica cells were observed in *Spartina* and *Tragus*, being more common in the latter.

Bicellular microhairs. Chloridoid microhairs were observed in all species of *Leptochloa* except *L. ciliolata*, *Diplachne cuspidata*, and *L. decipiens*. Microhairs generally were scattered, but in *Leptochloa caudata* and *L. longa* they were common near the apex. The basal cells of microhairs of *Leptochloa panicoides* (Fig. 47) and *L. viscida* (Fig. 53) were atypically thick and nontapering toward their basal insertion. Additional study is needed to evaluate whether the shape of the basal cell can be hypothesized as a separate character.

Among OET, seven eleusinioid genera had panicoid microhairs (*Ectrosia gullivieri*, *Habrochloa*, *Heterachne*, *Neyraudia*, *Steirachne*, *Triraphis*, *Viguierella*), whereas the remaining OET had chloridoid microhairs. Microhairs were not observed in *Cladoraphis spinosa* or *Viguierella*, the latter of which needs further study, since only one specimen was available for study (Table 1). As with species of *Leptochloa*, microhairs varied in abundance and were generally scattered; only near the apex in *Apochiton* and *Triraphis* were they common. Nicora (1962: 9) illustrated enneapogonoid microhairs in Eleusininae for *Neeragrostis*, which Clayton and Renvoize (1986) included in *Eragrostis*. The enneapogonoid microhairs observed here for *Cladoraphis cyperoides* and *Psammagrostis wiseana* (Fig. 65) represent only the second report for this type in Eleusininae. All microhairs in *Psammagrostis* (Fig. 65) had swellings distal to the base of the microhair, a condition not observed elsewhere.

All OERG had chloridoid microhairs.

Papillae. Papillae occurred singly on short cells or singly on the distal ends of long cells. Three clarifications are needed prior to presenting observations of papillae.

First, the distal ends of the outer walls of epidermal *long* cells can be noticeably swollen, as in *Eragrostiella* (Fig. 20), *Indopoa* (Fig. 26), and *Leptochloa virgata* (Fig. 52). These swellings were recognized by Valdés-Reyna and Hatch (1991: fig. 23) in at least one instance as papillae. As I interpret them, outer walls that are merely swollen are distinct from true papillae. The distinction between long cells possessing a single, distal papilla (e.g., *Leptochloa coerulescens*, Fig. 31) and long cells that are merely swollen can be seen with *Leptochloa chinensis* (Fig. 29), in which a single papilla is evident atop the distal swelling of a long cell, and with *L. fusca* (Fig. 37), in which long cells are either papillate or merely swollen. Second, the outer wall of *short* cells prior to differentiation can appear rounded (papillate, fide Valdés-Reyna & Hatch, 1991) when viewed in profile (e.g., *Eragrostiella*, Fig. 20; *Indopoa*, Fig. 26). The rounded outer walls should not be confused with papillae, which are localized processes arising from the outer wall. Third, the apical extensions of the lateral walls of long cells of *Leptocarydion* (Fig. 28) and *Steirachne* (Fig. 69) are distinct from true papillae; Palmer and Gerbeth-Jones (1988: 94) have noticed a similar distinction in *Phacelurus* (Panicoideae, Andropogoneae), as did Peterson (1989) in *Muhlenbergia* (Chloridoideae, Sporobolinae). Thus, for this study papillae are taken to be apically rounded, undifferentiated processes that arise from and are localized on the outer cell wall, and which can become silicified (Clark & Gould, 1975; Terrell & Wergin, 1981; Consaul & Aiken, 1993). (Ellis (1979) cited Metcalfe (1960) that papillae can become cutinized. However, Metcalfe (1960: 668) indicated only one species (*Trikeraia hookeri* (tribe Stipeae)) as having cutinized papillae. Furthermore, Metcalfe (1960) did not indicate how he determined the presence of cutin.) It is important to stress that other structures on grasses called papillae may not be

homologous to the papillae described here (Clark & Gould, 1975; Zuloaga, 1987: fig. 26.2c; Dávila & Clark, 1990; Filgueiras et al., 1993; Jenks et al., 1994).

Papillae on short cells. Papillae on short cells occurred in several species of *Leptochloa* (*L. fascicularis, L. fusca, Diplachne gigantea, D. muelleri, L. panicoides, L. uninervia,* and *L. viscida*). In most cases they had a collapsed appearance, which may have been an artifact of preparation, or, since the silicification of papillae has been documented (Clark & Gould, 1975; Terrell & Wergin, 1981; Consaul & Aiken, 1993), perhaps was an indication that silica deposition had not occurred. Collapsed papillae on short cells are frequent in the literature (e.g., Palmer & Gerbeth-Jones, 1986: pl. 15a–f).

Relatively few OET had papillae on short cells (*Dinebra* spp.; *Drake-Brockmania* spp., Fig. 16; *Halopyrum,* Fig. 23; *Orinus,* Fig. 61). Only in *Halopyrum* (Fig. 23) were the papillae large. Unlike Valdés-Reyna and Hatch (1991) I did not detect papillae on short cells of *Eleusine* (not shown).

Among OERG, only *Tragus* (not shown) had papillae on the short cells.

Papillae on long cells. In the 13 species of *Leptochloa* having a single papilla on the long cells (Table 1) the papillae were more frequently present near the apex of the lemma. *Leptochloa fusca* (Fig. 37) and *Diplachne parviflora* (not shown) were inconsistent in this feature even over localized portions of the lemma; some long cells had papillae, others did not. *Leptochloa viscida* (Fig. 53) had only a few papillae near the lateral veins. The size of the papillae arising on long cells was more or less constant within *Leptochloa,* with the exception of *L. coerulescens* (Fig. 31), in which the papillae were noticeably longer. In some cases the papillae were weakly developed, as in *Diplachne cuspidata* (not shown) and *Diplachne gigantea* (Fig. 38).

Although many OET had long cells with swollen ends (e.g., *Bewsia,* Fig. 3; *Coelachyrum yemenicum,* Fig. 12; *Trichoneura,* Fig. 70, in part; compare with *Coelachyrum poiflorum,* Fig. 10, in which the long cells have no swellings), relatively few had a single papilla on the long cells (*Dinebra,* Fig. 15; *Drake-Brockmania,* Fig. 16; *Kengia,* Fig. 27; *Odyssea,* Fig. 60, not visible; *Orinus,* Fig. 61; and *Oropetium,* Fig. 62). The significantly greater basal diameter of papillae in *Halopyrum* differs from other taxa in Eleusininae.

Long cells with papillae were absent in the OERG.

Prickles. Prickles were observed in every species of *Leptochloa* and tended to increase in frequency toward the apex. Among *Leptochloa* species prickles were rare in *Diplachne cuspidata, L. digitata, L. mucronata, L. rupestris, L. uniflora,* occasional in most species, or common, as in *L. caudata.*

Prickles were observed for all OET. A single prickle was observed on *Psilolemma*; however, since only one was observed on three specimens, and because its apex was directed toward the lemmatal base (almost universally they point toward the apex in Eleusininae), it was considered an abnormality and recorded as absent. Prickles were most abundant in *Cladoraphis* spp. (Figs. 6, 7), *Ectrosia* spp. (Figs. 17, 18), *Gouinia* (Fig. 21), *Halopyrum* (Fig. 23), and *Oropetium* (Fig. 62). Unlike Valdés-Réyna and Hatch (1991), prickles were observed (with a dissecting microscope) on herbarium specimens of *Tridens* spp., *Vaseyochloa multinervosa,* and *Triplasis purpurea,* although they were occasionally only infrequently present at the apex.

Prickles occurred on all OERG. *Spartina* (not shown) had prickles of widely different sizes. Prickles were generally most abundant on the awns of species bearing these structures (e.g., *Lintonia,* Fig. 54); in *Pogoneura,* prickles were restricted to the awn.

Macrohairs. All species of *Leptochloa* had at least some macrohairs on the lemmas. They were not observed using SEM on *Diplachne gigantea,* but analysis of an isotype (*Vesey-Fitzgerald 1551*; BM) with a dissecting microscope revealed the presence of short macrohairs along the edges of the midrib of some lemmas. In some species they are rare, such as the sparse basal occurrence on *Leptochloa digitata* (Fig. 32). Most macrohairs observed in *Leptochloa* were typical in having smooth edges and a rounded or acute tip. However, a "clavicorniculate" type (see Discussion) was found in *D. eleusine,* in which the subapical portion was noticeably clavate, and above which occurred a corniculate tip. This feature was noted earlier by Phillips (1974, 1982) for *D. eleusine, Coelachyrum yemenicum, Lintonia,* and *Trichoneura.* The hairs shown for *Tribolium obliterum* by Visser and Spies (1994: fig. 3b) may be clavicorniculate, but this is uncertain since only their apices are shown.

A majority of OET had macrohairs on the lemma; they were absent in *Acrachne* (Fig. 1), *Cladoraphis spinosa* (Fig. 7), *Desmostachya* (Fig. 14), *Ectrosia leporina* (Fig. 18), *Ectrosiopsis* (Fig. 19), *Eleusine* (not shown), *Eragrostiella* (Fig. 20), *Heterachne* (Fig. 25), *Myriostachya* (Fig. 56), *Psilolemma* (Fig. 66), *Sclerodactylon* (Fig. 68), *Steirachne* (Fig. 69), and *Viguierella* (Fig. 72). Only two macrohairs were observed at the very base of one specimen (*Faden et al. 74/613,* Appendix 1) of *Harpachne schimperi.*

The study of several herbarium sheets at MO revealed that a few macrohairs occasionally occur on the edges near the base of some lemmas. However, they are at most infrequent and are always relatively short. Moreover, given their length, one could just as easily designate them as (relatively long) prickles. Examination of specimens of *H. bogdanii* (MO: *Heady 1466*, *Bogdan 4524*), the other species in the genus, also revealed a few short hairs near the base of some lemmas. Given their sporadic occurrence and their questionable status as hairs (vs. relatively long prickles), I have recorded them as present or absent (Table 1). The abundant macrohairs on *Apochiton* (Fig. 2) made observation of other features difficult. The clavicorniculate hairs of *Coelachyrum yemenicum* appear identical to those of *Diplachne eleusine*. A crispate macrohair, identifiable by the irregular ("crisped") surface and apparently reported here for the first time in grasses (Uphof, 1962; Metcalfe, 1960; Ellis 1976, 1979), was observed for *Coelachyrum brevifolium* (Fig. 8), *C. poiflorum* (Figs. 9, 10), and *C. stoloniferum* (Fig. 11). The crisping is expressed most thoroughly toward the apex, and somewhat less so basally. Some macrohairs of *Trichoneura grandiglumis* (Fig. 70) were swollen at the base.

Among the OERG surveyed, only *Spartina* lacked macrohairs. Some specimens of *Cynodon nlemfuensis* (Fig. 13) had macrohairs with distinctly "apiculate" (sensu Peterson, 1989) tips.

Discussion

This study originated from morphologically based cladistic studies of *Leptochloa* using various combinations of likely sister genera, as hypothesized by Clayton and Renvoize (1986). The sole use of gross morphology gave poorly resolved consensus trees and clades with low support values (Snow, unpublished). Moreover, the use of a single data set may have resulted in artificial groupings, a potential problem Hilu and Wright (1982) alluded to in their phenetic study of chloridoid grasses. These factors suggested that additional characters might lead to more "accurate" (sensu Hillis & Bull, 1993) estimations of the phylogenetic relationships. Given that micromorphological characters have known systematic value in grasses (references in Introduction), this study was undertaken to enlarge extant data sets for purposes of phylogenetic inference.

Cork Cells. Given their universality in *Leptochloa*, cork cells are of no phylogenetic value in the genus.

However, the variable presence of cork cells in Eleusininae and Eragrostideae suggests they are phylogenetically informative at the generic level. Cork cells were recorded as present only when the short cell was substantially darkened (as viewed by SEM), whereas Palmer and associates generally recorded cork cells as present when any undifferentiated short cell occurred adjacent to a silica cell (e.g., Palmer et al., 1985: pl. 1e, 2e, 3e, 4c, and many others therein). I agree with J. T. Columbus (pers. comm., January 1995) that the extent to which suberin deposition actually occurs, and the extent to which it can be observed, needs further investigation. If suberin deposition in short cells is eventually demonstrated to be invisible to SEM, or it is shown that "cork cells" on lemmas are lacking in suberin, then their use as phylogenetic markers will need reconsideration. These considerations aside, I have followed others (e.g., Valdés-Reyna & Hatch, 1991) by recording cork cells as either present or absent.

Silica Cells. Lemmatal silica cells were mostly absent from *Leptochloa*, and thus have minimal infrageneric phylogenetic value. Since only one specimen of *L. fascicularis* (Fig. 35) had a few silica cells, their occurrence on that specimen is probably similar to lemmatal stomata, which occasionally reappear as atavisms from the transformationally antecedent leaves. However, in *Leptochloa monticola* (Fig. 41) silica cells are common, which requires a reassessment of earlier research. Using several lines of evidence, Valls (1978) suggested that *L. monticola* was generically misplaced. Based on leaf anatomy and citing Clifford and Watson (1977), Valls (1978) suggested a possible alliance with *Chionochloa* Zotov (Arundinoideae, Arundineae). To assess a possible alliance with Arundineae, I sampled lemmas from *Chionochloa conspicua* (Forst. f.) Zotov subsp. *cunninghamii* (Hook. f.) Zotov, *C. flavescens* Zotov, *Danthonia dominguensis* Hack. & Pilg., and *Rytidosperma pilosum* (R. Br.) Connor & Edgar (Appendix 1; data not shown). Unlike *L. monticola*, which had chloridoid microhairs, the microhairs of *C. conspicua* var. *cunninghamii* and *R. pilosum* were panicoid; furthermore, microhairs were not seen for *C. flavescens* or *D. dominguensis*. Of relevant note, Watson and Dallwitz (1992) reported panicoid microhairs (for the abaxial leaf surface) for *Danthonia*, which does not accord with the chloridoid microhairs of *Leptochloa monticola*. In addition, the species of *Chionochloa* lacked cork cells, which were present in *L. monticola*. Morever, the dumbbell-shaped silica bodies in *L. monticola* differed from the saddle-shaped silica bodies of *C. flavescens* and *D. dominguensis*. Whereas each of these taxa has at least one discrepancy when compared to *L. monticola*, lemmatal

micromorphology alone does not support an obvious relationship of *L. monticola* to Arundineae.

Saddle-shaped (Clifford & Watson, 1977; Valls, 1978), dumbbell-shaped (Valls, 1978), and cross-shaped (Metcalfe, 1960) silica bodies have been reported for leaf blades in *Leptochloa.* Valls (1978: 82) has shown that both dumbell-shaped and saddle-shaped silica bodies occur in *Leptochloa dubia.* Ovate and saddle-shaped silica bodies were observed for *Odyssea mucronata.* The presence of two shapes of silica bodies on *L. dubia* and *O. mucronata* cautions against their uncritical use as diagnostic or phylogenetic markers. Recognition of shape differences of silica bodies as distinct characters (or character states) thus seems premature until it can be demonstrated that infraspecific variation in silica body shape is minimal. This caveat is supported by studies in *Oryza* (Whang & Kim, 1994) and *Zizania* (Terrell & Wergin, 1981) (both genera in tribe Oryzeae), which documented extensive infraspecific variation in the shape of silica bodies.

Ignoring for the moment silica body shape, and focusing on mere presence or absence, silica cells appear to be important phylogenetic markers, since they were not observed in over half of the OET and OERG examined. Their presence on the lemma is probably symplesiomorphic, given the near universal occurrence of silica bodies in grass leaves, and that the lemma is transformationally homologous to the leaf. Testing for parallel loss or gain, however, will require a cladistic approach (Snow, in prep.).

Bicellular microhairs. The lack of microhairs (e.g., *Leptochloa ciliolata, Diplachne cuspidata, L. decipiens*) is not unequivocal evidence for their absence, since a single microhair was often all that was visible for three or more specimens of a given taxon. Microhairs were not restricted to certain portions of the lemma, but, when infrequent, were usually found near the apex. In some taxa, such as *Lintonia,* they extend onto the awn. Given a simple presence or absence, microhairs probably would be of little phylogenetic value in Eleusininae. However, two features of microhairs suggest their utility as systematic markers. First, Amarasinghe and Watson (1988) demonstrated that ten chloridoid genera, including *Leptochloa,* have partitioning membranes in the basal cell of the microhair. Moreover, the membranes were limited to the subfamily Chloridoideae (Amarasinghe & Watson, 1988: 307). Of the genera they surveyed in Eleusininae, *Eragrostis, Pogonarthria,* and *Triraphis* lacked the membranes. The use of partitioning membranes as a potential phylogenetic marker in the subfamily merits further investigation over a wider range of taxa. Second, with few exceptions (e.g., *Eragrostis,* Watson & Dallwitz, 1992), microhairs can be readily assigned to one of three morphological types: chloridoid, panicoid, or enneapogonoid, based on morphological differences of the basal and distal cells and their length ratios (Tateoka et al., 1959; Jacobs, 1987; Amasaringhe & Watson, 1988; Watson & Dallwitz, 1992; but see below also).

The elongated aspect and thin wall of the distal cells in the microhairs of seven OET (e.g., *Habrochloa,* Fig. 22) characterize them as panicoid microhairs (Table 1), which in all cases accords with the observations of Watson and Dallwitz (1992) for leaves.

The discovery of enneapogonoid microhairs on the lemmas of *Cladoraphis cyperoides* and *Psammagrostis wiseana* represents the third report of enneapogonoid microhairs outside the tribe Pappophoreae (Chloridoideae) and the second in Eleusininae. They were first reported for *Amphipogon strictus* (Arundinoideae) by Amarasinghe and Watson (1988). Earlier, Watson and Dallwitz (1992: 232) were unable to find microhairs on leaf blades of *C. cyperoides* from photographic material provided by R. P. Ellis. Of the bicellular microhairs illustrated by Tateoka et al. (1959), the microhair of *C. cyperoides* seems to most resemble those of *Sporobolus vaginiflorus* (Tateoka et al., 1959: fig. b,64) and *Pappophorum elegans* (Tateoka et al., 1959: fig. b,155). It also somewhat resembles a microhair reported by Peterson (1989: fig. 2,d) for two species of *Muhlenbergia.* The swelling distal to the base of the microhairs in *Psammagrostis* (Fig. 65) was absent elsewhere in Eleusininae.

Although not identified as such, an enneapogonoid microhair was recently shown for the arundinoid species *Pentameris distichophylla* (Barker, 1993: fig. 1,c). The recognition of three morphological categories of microhairs admittedly represents typological thinking, which can misguide the understanding of biological reality (Mayr, 1982). Thus, when making preliminary hypotheses of homology (de Pinna, 1991), one might consider whether the "enneapogonoid" microhairs of *Cladoraphis cyperoides* and *Psammagrostis wiseana* are homologous with those occurring in *Enneapogon,* or whether the relative elongation of the basal cell is a "character" itself, the elongation having been achieved independently from the enneapogonoid type. Overall, the distinct morphologies of microhairs in Eleusininae and their tendency to be restricted generically together suggest their potential value as indicators of phylogenetic relationships.

Papillae. The characterization and interpretation of papillae were initially confounded by several

factors (see Results). Despite the more restricted criteria given above, the presence or absence of papillae is probably of phylogenetic value in *Leptochloa* and other genera in Eleusininae. The papillae on short cells were almost always collapsed, and thus could be confused with the collapsing outer wall of short cells, which apparently occurs during suberin deposition of cork cells (see above). That these structures could rightly be called papillae only suggested itself after repeated comparisons between numerous photos of taxa with and without this feature, and seeing similar photos of collapsed papillae in the literature. The papillae on short cells are perhaps best revealed on *Drake-Brockmania somalensis* (Fig. 16).

All members of the *Leptochloa fusca* group (tentatively: *Diplachne cuspidata, L. fascicularis, L. fusca, Diplachne gigantea, D. muelleri, D. parviflora, L. uninervia*) have a single papilla located distally on long cells, as well as having some short cells with a single papilla. Other characters that suggest a close relationship among its members include an apically attenuated ligule, relatively long spikelets, spikelets with frequently five or more florets, the perisperm of the caryopsis being only weakly adnate to the endosperm, and a pronounced lacuna in the midvein of the leaf blade (Snow, in prep.). *Leptochloa chinensis* and *L. coerulescens*, which both have papillae on long cells, have not been previously hypothesized to be closely related. Many species of *Leptochloa* have never been apportioned into subgenera or sections, but based on Clayton and Renvoize (1986), papillate species that would be placed in section *Diplachne* include the *L. fusca* group, *L. panicoides*, and *L. viscida*, whereas other papillate species would be placed in section *Leptochloa*. Papillae on short cells are also known from *Festuca* (Consaul & Aiken, 1993) and other genera in Pooideae (Thomasson, 1986).

Of the Eleusininae genera studied herein reported to have papillae (Valdés-Reyna & Hatch, 1991), I observed them only in some species of *Leptochloa*. This is due to the different interpretation of papillae used for this analysis (Results). The papillae of *Halopyrum*, which have a larger basal diameter than related genera, approximate a condition found in some genera of other subfamilies (e.g., *Brachiaria* (Panicoideae, Paniceae), Zuloaga & Soderstrom, 1985; fig. 2d; *Olyra* (Bambusoideae, Olyreae), Soderstrom & Zuloaga, 1989; fig. 21c), in which the entire outer wall swells outward, thus making more difficult the distinction between papillae and swollen outer walls.

Among OERG, I was unable to determine whether *Tragus* had papillae on short cells, since distinguishing between long and short cells was difficult; this uncertainty is reflected by the question mark in Table 1.

Prickles. Whereas Valdés-Reyna and Hatch (1991) did not observe prickles in their sample of *Leptochloa*, I found a universal occurrence of prickles in the genus. Given their universality and assuming that *Leptochloa* is monophyletic, they have no phylogenetic value. Others have suggested that the location of micromorphological characters (e.g., costal vs. intercostal zones) should be noted (Ellis, 1979; Consaul & Aiken, 1993). However, no obvious differences in costal and intercostal zones were noted for *Leptochloa*. Peterson (1989) differentiated between regular prickles and apiculate prickles in some species of *Muhlenbergia*, but this distinction did not hold in *Leptochloa*, OET, and OERG (but see comments below under macrohairs).

The phylogenetic value of prickles is similar for OET, since only *Psilolemma* was lacking this character. Species of *Trichoneura* and *Tripogon* studied by Valdés-Reyna and Hatch (1991) lacked prickles, but I observed them in other species of these genera (Table 1). As documented so thoroughly by Dávila and Clark (1990) for leaf blade epidermal micromorphology, all species need to be sampled to fully assess the occurrence of prickles and other micromorphological features within a genus.

That the size of prickles could vary on a lemma is most evident in *Spartina* (not shown), in which prickles on the margin of the lemma dwarfed those in the intercostal zones. Sizable differences were also evident in *Apochiton, Cladoraphis spinosa, Dinebra retroflexa* (Fig. 15), *Leptochloa longa, L. nealleyi* (Fig. 44), and *L. scabra*. Others have found discrepancies in lemmatal or laminar prickles within a species (Prat, 1948: his large and small "spicules"; Davies, 1959: his "asperities" and "incipient asperities"; Ball et al., 1993: compare fig. 1 with fig. 8; Thomasson, 1986: fig. 15, and note the increasing size of prickles between figs. 2, 5, and 7; Barker, 1993: fig. 2a–d).

In several cases prickles were flat at the base or had weak conduplicate basal folding (present but not shown in: *Orinus, Leptochloa fascicularis, L. monticola, Diplachne muelleri*), a condition illustrated (Zuloaga, 1987: fig. 26.4d; Thomasson, 1986: figs. 4, 17; Valdés-Reyna & Hatch, 1991: fig. 44) and discussed (Consaul & Aiken, 1993: 1656) earlier for other taxa. The conduplicate condition may be an early expression of prickle ontogeny in which the outer wall evaginates prior to its expansion, after which silica deposition may occur and the rigidity of the prickle is achieved. The accumulation of silica in the tips of prickles (Consaul & Aiken,

1993) probably explains their brittleness and propensity to break (e.g., *Gouinia, Kengia* (Fig. 27)).

Two categories of prickles (prickles and hooks) have historically been recognized (Metcalfe, 1960; Ellis, 1979). The tendency to distinguish between hooks and prickles reflects the frequent occurrence on specimens of two distinct sizes of projections of the outer wall (e.g., Palmer & Gerbeth-Jones, 1986: pl. 10a,c & pl. 12c,f; Dávila & Clark, 1990: fig. 34). Since the distinction between them seems absolutely arbitrary *within Eleusininae* (e.g., note gradations in *Dinebra retroflexa,* Fig. 15), I have chosen not to recognize hooks. Metcalfe (1960) suggested that hooks were homologous with prickles. His use of the term homology was probably invoking the concept of intermediate forms (Remane, 1952; Sattler, 1984), which illustrates their common developmental trajectories, and which according to some intepretations of homology (de Queiroz, 1985) establishes their homology. Ellis (1979: 668) indicated that prickles on leaf blades originate from short cells, but prickles clearly also arise from long cells of lemmas on *Gouinia* (Fig. 21), *Kengia, Leptochloa monticola* (Fig. 41), *Lintonia* (Fig. 54), and *Pogonarthria* (Fig. 63). If prickles continue to be recognized as characters distinct from macrohairs (but see below), it will be necessary to recognize that prickles can arise from either short cells (Ellis, 1979) or long cells (this study).

Macrohairs. Ellis (1979) has stated that macrohairs arise from long cells. Kellogg (1990: 1983) noted that the arachnose lemmatal hairs of *Poa* appear to initiate from short cells, but only because those cells have not yet elongated into long cells. My observations indicate that macrohairs can arise from long cells or short cells. Their origin from short cells is most evident in *Bewsia* (Fig. 3), *Leptochloa fasicularis* (Fig. 36), *L. neesii* (Fig. 45), and *Neesiochloa* (Fig. 57). On long cells, they can arise from the proximal end, as is evident in *Coelachyrum yemenicum* (Fig. 12), *Diplachne eleusine* (Fig. 34), *Trichoneura* (Fig. 70), *Triraphis* (Fig. 71), or rarely on the distal end, as for example in *L. mucronata* (Fig. 42).

In *Leptochloa* spp., normal macrohairs were generally restricted to the lower and middle portions of the nerves. A clavicorniculate type was observed for *Diplachne eleusine* (Fig. 34), which was also present in *Coelachyrum yemenicum* (Fig. 12). Phillips recognized clavicorniculate hairs for both *D. eleusine* and *Coelachyrum yemenicum* (as *Cypholephis yemenica*), calling them "club-shaped" (Phillips, 1974) and later "clavate" (Phillips, 1982: 155). Since the hairs have a distinctly narrowed portion above the subapical swelling, the clavicorniculate designation seems to best describe their morphology. (The assistance of D. Nicolson in matters of terminology is here acknowledged.) Clayton and Renvoize (1986) distinguished *Leptochloa* from *Coelachyrum* in part by the broadly elliptic, concavo-convex, rugulose caryopsis of the latter. The inflorescence of *Diplachne eleusine* resembles that of *C. yemenicum* in having few, relatively short, and more or less erect spicate branches. In addition, the caryopsis characters of the two species are similar in outline and cross-sectional shape, and in having a smooth pericarp that is weakly adnate to the endosperm (Snow, unpublished). Like most species of *Leptochloa* and unlike most species of *Coelachyrum,* the grain of *C. yemenicum* is not rugulose. Watson and Dallwitz (1992) segregated *C. yemenicum* into the monotypic genus *Cypholepis* and mentioned the presence of clavicorniculate hairs. Phylogenetic studies are needed to determine the generic affinites of *D. eleusine* and *C. yemenicum,* but the above evidence, along with cladistic studies by Van den Borre (1994: 216), suggests they may be phylogenetically close.

This study is the first to document the crispate macrohair, which occurs in *Coelachyrum breviflorum* (Fig. 8), *C. poiflorum* (Figs. 9, 10), and *C. stoloniferum* (Fig. 11). It is characterized by an irregular wrinkling (crisping) of the surface, which is expressed most fully toward the apex. That the wrinkling was found repeatedly in these taxa and not elsewhere suggests it was not an artifact of preparation. In grasses, the morphological "type" most resembling the crispate type is that of *Danthoniopsis viridis* (Panicoideae, Arundinelleae), which has a sparsely papillate shaft (Palmer & Tucker, 1981: fig. 9f). It differs from the crispate type in that significant portions of the shaft are relatively smooth. Infrequent and irregular papillate bulges on the shaft of macrohairs have been noted sporadically on the lemmas of *Neostapfia colusana* Davy and *Orcuttia pilosa* Hoover (Snow, unpublished), both members of the tribe Orcuttieae (Chloridoideae). Trichomes having micropapillate wall sculpturing were reviewed by Uphof (1962) and recently have been noted in Rubiaceae (Sullivan, 1986) and Verbenaceae (Rueda, 1994). The exclusive occurrence of crispate macrohairs in three species of *Coelachyrum* suggests it is a synapomorphy at some level in that genus.

As mentioned above, Peterson (1989) used the term "apiculate" to distinguish between the apices of prickles in some species of *Muhlenbergia.* This distinction is useful for the apices of some macrohairs. The apices of macrohairs in two specimens (*Crook 2115, Gereau et al. 3490*) of *Cynodon nlem-*

fuensis (Fig. 13) were noticeably apiculate in comparison to other taxa (Appendix 1). The possible systematic significance of apiculate tips warrants further attention.

Peterson (1989) also recognized "swollen base" macrohairs in some species of *Muhlenbergia*. Some, but not all, macrohairs of *Trichoneura grandiglumis* (Fig. 70) had this feature. Macrohairs with swollen bases may arise from long cells, which have a larger foundation relative to short cells. Future research should evaluate whether macrohairs have normal or swollen bases.

It is important to distinguish between the base of the macrohair and the surrounding cells that can swell outward to buttress the macrohair at its base (Ellis, 1979: 657). Swollen cells adjacent to lemmatal macrohairs have been called (collectively) tubercles or papillate bases, and were noted in OET only for *Richardsiella* (Fig. 67) and in OERG for *Tragus* (not shown). The tubercles were much larger in *Richardsiella*.

Like prickles, the basal portion of some macrohairs was distinctly flattened or somewhat conduplicate, as in *Bewsia* (Fig. 3), *Chloris verticillata* (Fig. 5), *Coelachyrum yemenicum* (Fig. 12), *Leptochloa neesii* (Fig. 45), and *L. squarrosa* (Fig. 50). This condition is evident in some macrohairs of the unrelated genus *Olyra* (Soderstrom & Zuloaga, 1989: fig. 6c). Ontogenetic stages of macrohair elongation can be seen with three closely spaced hairs on *Chloris verticillata* (Fig. 5). As with prickles, the outer wall of the cell appears to evaginate in a conduplicate manner and flatten as the macrohair begins development. Although most fully developed macrohairs lack the folded base, the base sometimes remains flattened (*Coelachyrum yemenicum*, Fig. 12; *Leptochloa neesii*, Fig. 45; *L. squarrosa*, Fig. 50; and *Neesiochloa*, Fig. 57). The base of macrohairs can be hollow, as evidenced by basally severed hairs in *Leptochloa fusca* (Fig. 37) and *Ochthochloa* (Fig. 59).

Phylogenetic utility of lemmatal micromorphology. Micromorphological characters generally vary little in *Leptochloa*. With few exceptions, cork cells were present, silica cells were absent, chloridoid bicellular microhairs were present, prickles were present, and macrohairs were present. The occurrence of papillae on long cells and short cells was more variable, suggesting their presence or absence may be phylogenetically informative within the genus.

In addition to *Leptochloa*, seven genera were studied for two or more species. Overall, little intrageneric variation was generally observed for given characters. For example, only *Odyssea* varied in its expression of cork cells (Table 1). As so thoroughly documented by Dávila and Clark (1990) for the leaf blades of *Sorghastrum*, a complete survey of all species is necessary to fully characterize a genus. So, although further study is needed, it appears that lemmatal micromorphological characters within genera of Eleusininae are largely conservative. However, as evident from Table 1, significant variation occurred between genera. As such, micromorphological characters are probably reliable phylogenetic markers at the generic level.

Micromorphological characters and problems of homology. The micromorphological characters in this study have been reported and discussed following the tradition of Metcalfe (1960) and Ellis (1979). That is, cork cells, silica cells, bicellular microhairs, papillae, prickles, and macrohairs have been treated separately, without questions having been raised about their ontological status as distinct characters. However, abundant evidence from the literature suggests that papillae, hooks, prickles, and macrohairs often represent arbitrary stages along one or two developmental trajectories. (If we recognize the fundamental difference between long and short cells, and if we therefore choose to differentiate between the outward extensions of the outer cell walls of short cells vs. long cells (into papillae, hooks, prickles, macrohairs), then one might argue that there are separate developmental trajectories for outer cell wall extensions of short and long cells.)

Confounding matters has been an inconsistency in the previous use of terminology. As one of many examples, the cupulate papillae in *Muhlenbergia* (subfamily Chloridoideae; Peterson, 1989) resemble the hooks of some *Melica* spp. (subfamily Pooideae; Thomasson, 1986). This may simply reflect differences in papillae at the subfamilial level, or suggest that papillae between the two subfamilies are not homologous. As a second example, most agrostologists have seen the gradual transition that occurs in the axils of the primary branches on the rachis from "prickles" to "macrohairs." Such transitions are easily found on individual specimens. Statements such as

> . . . it seems probable that those [prickles] that eventually become pointed may pass through an unbarbed phase [i.e., papillae and/or hooks] during their ontogenetic development, but this possibility needs further investigation (Metcalfe 1960: xxiv)

and

> The distinction between macrohairs and prickles is often not clear . . . (Ellis 1979: 667)

suggest that the distinction between character and

character state is ambiguous, and illustrate the need for reconsidering the relationship between homology and ontogeny for these features.

Morden (1985: 36), upon examination of micromorphological characters on the lemma and palea of some species of *Muhlenbergia*, stated "The presence of papillae on the epidermis of the floret appears to represent the initiation of villous [i.e., macrohair] growth, whether or not elongation follows." The photomicrographs (Morden, 1985: figs. 12–19, 24–27) reveal that the papillae on immature florets (lemmas and paleas) are present in regions where macrohairs develop on mature florets. The thinning of epicuticular waxes on the elongating papillae (Morden, 1985: fig. 25) suggests that wax-covered papillae can elongate into macrohairs (given, it is assumed, some sort of genetic signal). However, since some grasses can have several papillae per cell (Metcalfe, 1960; Ellis, 1979), it is doubtful that all papillae represent early stages in the ontogeny of macrohairs.

To be used as phylogenetic markers, there must be no ambiguity surrounding the ontological status of characters. Regarding papillae, hooks, prickles, and macrohairs, it remains necessary to question which entitites can be meaningfully compared as homologous characters (Haszprunar, 1992), since gradations between "characters" can be seen on *individual* specimens: e.g., (1) between papillae and hooks (Thomasson, 1986: figs. 1, 4, 7, 12, 14); (2) between papillae and prickles (Dávila & Clark, 1990: fig. 29); (3) between papillae and macrohairs (Morden, 1985; discussed above); (4) between hooks and prickles (Thomasson, 1986: figs. 4, 15; Dávila & Clark, 1990: fig. 3); and (5) between prickles and macrohairs (Palmer & Gerbeth-Jones, 1988: pls. 9c, 10a, 28f; Valdés-Reyna & Hatch, 1991: fig. 36; Consaul & Aiken, 1993: fig. 23; Barker, 1993: fig. 2b). Given these observations, the distinctions between papillae, hooks, prickles, and macrohairs have been somewhat arbitrary at best.

Although the uncertain homology status of several micromorphological characters and their questionable value as phylogenetic markers should now be evident, it would be premature to assert that distinctions between them are always arbitrary, and that they thus hold no phylogenetic value. Rather, previous research and the results herein indicate the need for a thorough review of the ontological status of papillae, hooks, prickles, and macrohairs. If these features are not ontogenetically individualized structures that are comparable across taxic hierarchies, then their utility as phylogenetic markers is suspect. Their phylogenetic application needs to be evaluated in light of theoretical considerations of ontogeny and homology (e.g., Patterson, 1982; Roth, 1984, 1991; de Queiroz, 1985; Wagner, 1989a, b; de Pinna, 1991; Hall 1992, 1994) and will be the basis of a subsequent paper (Snow, in prep.).

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Appendix 1. Species, authorities, collectors, and country of origin of specimens studied. Order of taxa is alphabetical. Not all taxa are in subfamily Chloridoideae (see Discussion). Taxa scattered within *Leptochloa* with the generic abbreviation "*D.*" (for *Diplachne*) lack a valid combination in *Leptochloa*. All vouchers at MO unless an herbarium acronym follows the country of origin. Identifications of specimens were verified using: Bor, 1973; Clayton, 1972; Clayton et al., 1974; Cope, 1985a, b; Elffers & Kennedy-O'Byrne, 1957; Gibbs Russell et al., 1990; Gould, 1975; Judziewicz, 1990; McVaugh, 1983; Ortíz, 1993; Simon, 1993; Tsvelev, 1976; Tutin, 1980.

Acrachne racemosa (Roem. & Schult.) Owhi: *De Wilde 6876*, Ethiopia; *Patel & Kaunda 4259*, Malawi; *Crook 837*, Zambia. *Apochiton burttii* C. E. Hubb.: *Braun 226*, Tanzania; *Sabaya 83*, Tanzania; *Greenway & Kanuri 14445*, Tanzania.

Bewsia biflora (Hack.) Gooss.: *Strid 2911*, Zambia; *Davidse 5968*, South Africa; *Wild 1685*, Zimbabwe. *Bouteloua curtipendula* (Michx.) Torr.: *Palmer 31445*, U.S.A.; *Thomas 107107*, U.S.A.; *Goodding 2463*, U.S.A. *Brachychloa schiemanniana* (Schweick.) S. M. Phillips: *Balsinhas 1129*, Mozambique; *Elffers s.n.*, Mozambique (US).

Chloris paniculata Scribn.: *Stewart 260*; Cocos Island (Costa Rica). *Chloris verticillata* Nutt.: *Snow 5779*, U.S.A.; *Henderson 69-307*, U.S.A.; *Gould 7804*, U.S.A. *Chondrosum gracile* Kunth: *Beetle & Guzman M-5579*, Mexico; *García 6*, Mexico; *Thieret & Brandenburg 53242*, U.S.A. *Chionochloa conspicua* (Forst. f.) Zotov subsp. *cunninghamii* (Hook. f.) Zotov: *Gardner 3307*, New Zealand. *Chionochloa flavescens* Zotov: *Mason 2920*, New Zealand. *Cladoraphis cyperoides* (Thunb.) S. M. Phillips (85): *Davidse 33370*, South Africa; *Lavranos & Pehlemann 19640*, Namibia; *Goldblatt 4244*, South Africa. *Cladoraphis spinosa* (L. f.) S. M. Phillips: *Davidse 33301*, South Africa; *Bayliss 5732*, South Africa; *Davidse 33265*, South Africa. *Coelachyrum brevifolium* Hochst.: *Adam 21799-4*, Mauritania; *Dwyer 13928a*, Saudi Arabia. *Coelachyrum poiflorum* Chiov.: *De Wilde & De Wilde-Duyfjes 10617*, Ethiopia; *De Wilde & De Wilde-Duyfjes 7975*, Ethiopia; *Boulos & Getahun 11906*, Ethiopia. *Coelachyrum stoloniferum* C. E. Hubb.: *Wieland & Gahair 4010*, Somalia; *Wieland 4098*, Somalia. *Coelachyrum yemenicum* (Schweinf.) S. M. Phillips: *Ellis 2643*, Botswana; *Gilbert & Gilbert 2335*, Ethiopia; *Leistner 1315*, South Africa. *Cynodon nlemfuensis* Vanderyst: (89) *Gereau et al. 3490*, Tanzania; *Grant s.n.*, Kenya; *Crook 2115*, Zimbabwe.

Danthonia dominguensis Hack. & Pilg.: *Zanoni et al. 37703*, Dominican Republic. *Desmostachya bipinnata* (L.) Stapf: *Fosberg 56909*, Pakistan; *Matamir 7/8*, Egypt; *Dwyer 13120*, Saudi Arabia. *Dinebra polycarpha* S. M. Phillips: *Ndegwa 639*, Kenya. *Dinebra retroflexa* (Vahl) Panz.: *Tanner 1430*, Tanzania; *Faden & Faden 74/741*, Kenya; *Schimper 1610*, Ethiopia. *Drake-Brockmania haareri* (Stapf & C. E. Hubb.) S. M. Phillips: *Mbano 5753*, Tanzania; *Drummond & Hemsley 2287*, Tanzania; *Bogdan 5434*, Kenya (US). *Drake-Brockmania somalensis* Stapf: *Heady 1815*, Kenya; *Faden & Faden 74/991*, Kenya; *Robertson 1755*, Kenya.

Ectrosia gulliveri F. Muell.: *Lazarides 4745*, Australia; *Blake 13574*, Australia. *Ectrosia leporina* R. Br.: *Clarkson 4892*, Australia; *Blake 18655*, Australia; *Clarkson 6059*, Australia. *Ectrosiopsis lasioclada* (Merr.) Jansen: *Lazarides 4787*, Australia. *Eleusine indica* (L.) Gaertn.: *Snow 5777*, U.S.A.; *Irwin et al. 11276*, Brazil; *Auquier 2142*, Zaire. *Eragrostiella bifaria* (Vahl) Bor: *Davidse & Sumithraarachchi 8991*, Sri Lanka; *Ash 648*, Ethiopia; *Faden & Faden 74/967*, Kenya.

Gouinia virgata (J. Presl) Scribn.: *Stevens & Moreno 18445*, Nicaragua; *Ventura 9239*, Mexico; *Seymour 3305*, Nicaragua.

Habrochloa bullockii C. E. Hubb.: *Webster T234*, Tanzania. *Halopyrum mucronatum* (L.) Stapf: *Ash 708-A*, Ethiopia; *Davidse & Sumithraarachchi 8224*, Sri Lanka; *Wingfield 4396*, Tanzania. *Harpachne schimperi* A. Rich.: *Davidse 9224*, Kenya; *Faden et al. 74/613*, Kenya; *Amshoff 6468*, Ethiopia. *Heterachne abortiva* (R. Br.) Hughs: *Must 1213*, Australia; *Clarkson 3700*, Australia; *Lazarides 9250*, Australia.

Indopoa paupercula (Stapf) Bor: *Santapau 10287*, India; *Santapau 10269*, India; *Saldanha 17978*, India.

Kengia serotina (L.) Packer: *Suza 655*, Czech Republic; *Svestka s.n. (MO 1743346)*, Czech Republic; *Clemens 1616*, China.

Leptocarydion vulpiastrum (De Not.) Stapf: *Ndegwa 655*, Kenya; *Crook 818*, Zimbabwe; *Van Jaarsveld 412*, South Africa. *Leptochloa aquatica* Scribn. & Merr.: *Hitchcock 674*, Mexico; *Arsène 5760-A*, Mexico. *D. caudata* K. Schum.: *Lewys Lloyd 1*, Tanzania; *Kingollah 39*, Kenya. *L. chinensis* (L.) Nees: *Yao Kan et al. 79280*, Japan (China?); *Hsu 1392*, Taiwan; *Davidse & Sumithraarachchi 9006*, Sri Lanka. *L. chloridiformis* (Hack. ex Stuck.) Parodi: *Pensiero & Vegetti 2752*, Argentina; *Venturi 5724*, Argentina. *L. ciliolata* (Jedwabn.) S. T. Blake: *Anderson 738*, Australia; *Blake 5860*, Australia; *Hubbard 3217*, Australia. *L. coerulescens* Steud.: *Adam 14030*, Senegal; *Adam 17175*, Senegal; *Adam 27799*, Liberia. *D. cuspidata* Launert: *Giess & van dor Wait 12632*, Namibia. *L. decipiens* (R. Br.) Stapf ex Maiden: *Blake 12707*, Australia. *L. dig-*

itata (R. Br.) Domin: *Chippendale & Constable 19009*, Australia; *Clemens 21*, Australia; *Lazarides 3797*, Australia. *L. divaricatissima* S. T. Blake: *Blake 10517*, Australia; *Johnson 410*, Australia; *Blake 19152*, Australia. *L. dubia* (Kunth) Nees: *Snow 5857*, U.S.A.; *Pringle 1027*, Mexico; *Renvoize & Cope 4240*, Bolivia; *Stuckert 17257*, Argentina. *D. eleusine* Nees: *Maguire 8398*, South Africa; *Giess 8422*, Namibia; *Brown & Shapiro 166*, South Africa. *L. fascicularis* (Lam.) A. Gray: *Snow 5811-A*, U.S.A.; *Davidse et al. 11647*, Brazil; *Wingfield 5867*, Venezuela. *L. fusca* (L.) P. Beauv. ex Roemer & Schult.: *Davidse & Sumithraarachchi 9174*, Sri Lanka; *Leippert 4606*, Namibia; *Davidse & Sumithraarachchi 9119*, Sri Lanka; *Clemens 1615*, China; *Hubbard & Winders 6405*, Australia. *D. gigantea* Launert: *Smith 1387*, Botswana. *L. ligulata* Lazarides: *Jacobsen E58*, Australia (BRI); *Thompson & Sharpe CHA293*, Australia (BRI); *Anderson 704*, Australia (BRI). *L. longa* Griseb.: *Croat 16903*, Panama; *Hitchcock 672*, Trinidad; *Davidse 2612*, Trinidad. *L. marquisensis* (F. Br.) P. M. Peterson & Judz.: *Wagner & Lorence 6222*, Marquesas; *Lorence et al. 6230*, Marquesas; *Perlman 10242*, Marquesas. *L. monticola* Chase: *Leonard 4751*, Haiti (B); *Ekman 3075*, Haiti (US); *Ekman 1576*, Haiti (US). *L. mucronata* (Michx.) Kunth: *Snow 5801-A*, U.S.A.; *Raveill 1813*, U.S.A.; *McKenzie 1160*, U.S.A. *D. muelleri* Benth.: *Lazarides 5329*, Australia. *L. nealleyi* Vasey: *Snow 5814*, U.S.A.; *Swallen 10267*, U.S.A.; *Thomas & Allen 123786*, U.S.A. *L. neesii* (Thwaites) Benth.: *Davidse & Sumithraarachchi 9180*, Sri Lanka; *Davidse 7466*, Sri Lanka; *Wirawan 657*, Sri Lanka. *L. obtusiflora* Hochst.: *Mhoro 1868*, Tanzania; *De Wilde 6449*, Ethiopia; *Verdcourt 1101*, Kenya. *L. panicea* (Retz.) Owhi: *McGusker 229*, Tanzania; *Reekmans 8750*, Burundi. *L. panicoides* (J. Presl) Hitchc.: *Snow 5790*, U.S.A.; *Summers & Hudson 4596*, U.S.A.; *Nelson et al. 3213*, Honduras. *D. parviflora* (R. Br.) Benth.: *Lazarides 4400*, Australia. *L. rupestris* C. E. Hubb.: *Wood 2848*, Yemen (BM); *Pappi 2960*, Eritrea (US). *L. scabra* Nees: *Snow 5795-A*, U.S.A.; *Pohl & Davidse 12062*, Honduras; *Davidse 2617*, Trinidad. *L.* sp. nov. (Snow, in prep.): *Davidse & Sumithraarachchi 9066*, Sri Lanka. *L. squarrosa* Pilg.: *Mwasumbi & Mponda 12671*, Tanzania; *Bond 144*, Tanzania; *Greenway 5096*, Tanzania. *L. uniflora* Hochst. ex A. Rich.: *Davidse & Ellis 5925*, South Africa; *Greenway et al. 14075*, Tanzania; *Ellis 2780*, Zimbabwe. *L. uninervia* (J. Presl) Hitchc. & Chase: *Snow 5789*, U.S.A.; *McDaniel & Rimachi 23074*, Peru; *Garcia & Quevedo s.n.*, Puerto Rico. *L. virgata* (L.) P. Beauv.: *Snow & Evans 4392-C*, U.S.A.; *Ramírez 1687*, Venezuela; *Irwin et al. 11332*, Brazil. *L. viscida* (Scribn.) Beal: *Snow 5817*, U.S.A.; *Thurber 45*, U.S.A.; *Wright 2044*, U.S.A. *L. xerophila* P. M. Peterson & Judz.: *Decker 637*, Marquesas. *Lintonia nutans* Stapf: *Faden & Faden 74-747*, Kenya; *Ndegwa 599*, Kenya; *Ngoni 319*, Botswana. *Lophacme digitata* Stapf: *Smook 1453*, South Africa; *Anderson 36*, South Africa.

Myriostachya wightiana (Nees ex Steud.) Hook. f.: *Davidse & Sumithraarachchi 9027*, Sri Lanka; *Davidse & Sumithraarachchi 9051*, Sri Lanka; *Griffith 6621*, India.

Neesiochloa barbata (Nees) Pilg.: *Harley et al. 16293*, Brazil; *Boyle 347*, Brazil; *Irwin et al. 31661*, Brazil. *Neyraudia reynauldiana* (Kunth) Kena ex Hitchc.: *Liu 890113*, China; *Levine 1812*, China; *Maxwell 86-218*, Thailand.

Ochthochloa compressa (Forssk.) Hilu: *Dwyer 13928*, Saudi Arabia; *Munro s.n.* (MO 2964652), India; *Stewart 1387*, India. *Odyssea mucronata* (Forssk.) Stapf: *Ash 708*, Ethiopia. *O. paucinervis* (Nees) Stapf: *Leydu 703*, Namibia; *Leistner 2262*, South Africa; *Ellis 2767*, South Africa. *Orinus thoroldii* (Stapf) Bor: *Younghusband 147*, Khamajong. *Oropetium aristatum* (Stapf) Pilg.: *Fay 5932*, Central African Republic; *Adam 31611*, French Guinea; *Adam 14998*, Sudan.

Pogonarthria fleckii (Hack.) Hack.: *Rodin 9073*, Namibia; *Goldblatt 1901*, Namibia; *Giess 11285*, Namibia. *Pogoneura biflora* Napper: *Greenway & Turner 10608*, Tanzania (PRE); *Greenway et al. 10620*, Tanzania (US). *Psammagrostis wiseana* C. A. Gardner & C. E. Hubbard: *J. Stretch s.n.*, Australia (CANB). *Psilolemma jaegeri* (Pilg.) S. M. Phillips: *Greenway 10288*, Tanzania; *Greenway & Kanuri 13530*, Tanzania; *Bullock s.n.* (MO accession 1819125), Tanzania.

Richardsiella eruciformis Elffers & Kenn.-O'Byrne: *Phipps & Vesey-Fitzgerald 3227*, Zambia; *Webster A340*, Zambia (two sheets at MO; I sampled accession 2324532). *Rytidosperma pilosum* (R. Br.) Connor & Edgar: *Gardner 1372*, New Zealand.

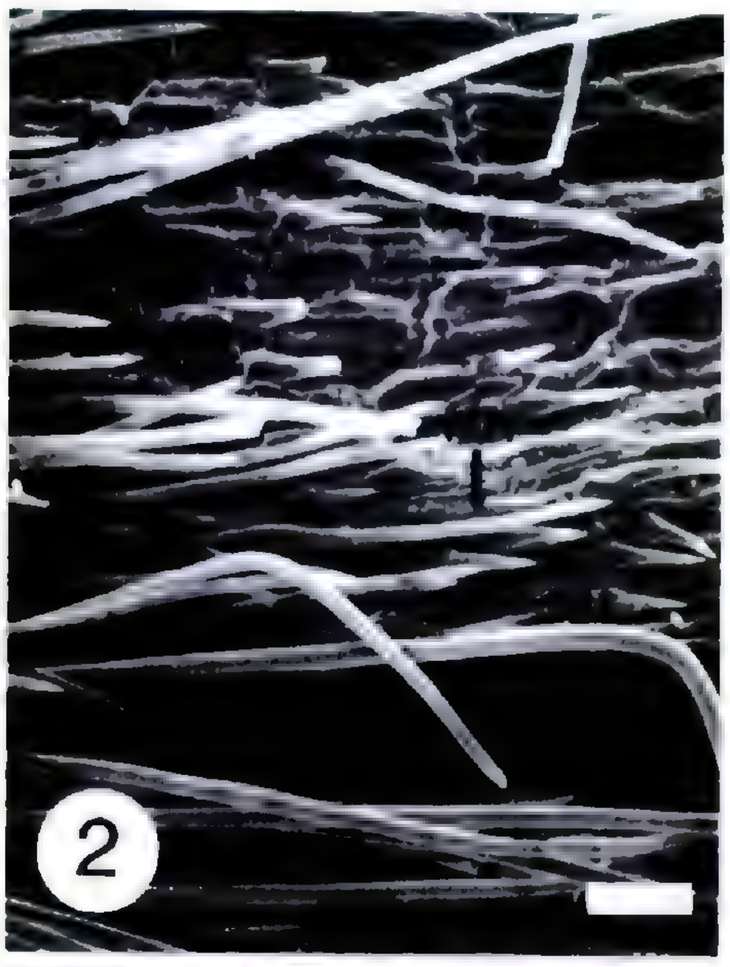
Sclerodactylon macrostachyum (Benth.) A. Camus: *Croat 30943*, Madagascar; *Fosberg 48752*, Aldabra Island (West Island). *Spartina pectinata* Link: *Hayden 11*, U.S.A.; *Conrad 10063*, U.S.A.; *Johnston 509*, U.S.A. *Steirachne barbata* (Trin.) Renvoize: *Stergios et al. 9733*, Venezuela; *Cuello 756*, Venezuela; *Maas & Westra 3771*, Guyana.

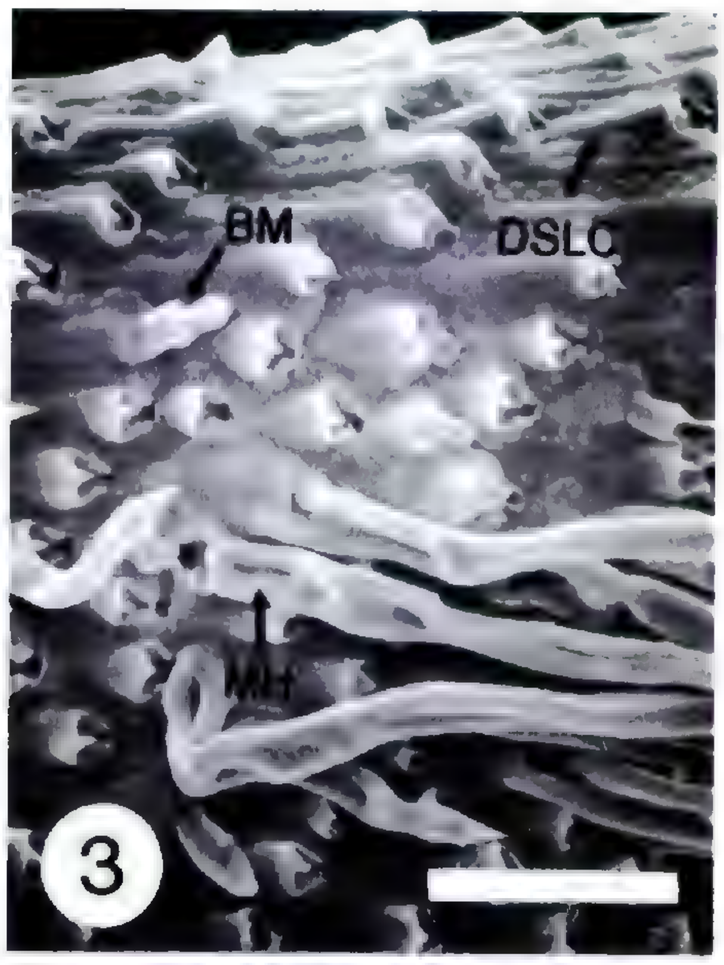
Tragus pedunculatus Pilg.: *Dinter 5698*, South Africa; *Ellis 2700*, South Africa. *Trichoneura grandiglumis* (Nees) Stapf & C. E. Hubb.: *Biegel 733*, Zimbabwe; *Ferreira F168*, South Africa; *Brain 1242*, Zimbabwe. *Tripogon major* Hook. f.: *Jacques-Georges 22087*, Sierra Leone; *Bogdan 3932*, Kenya; *Thulin & Mhoro 3040*, Tanzania. *Triraphis andropogonoides* (Steud.) E. Phillips: *Smook & Gibbs-Russell 2192*, South Africa; *Smook 3008*, South Africa; *Scheepers 1313*, South Africa.

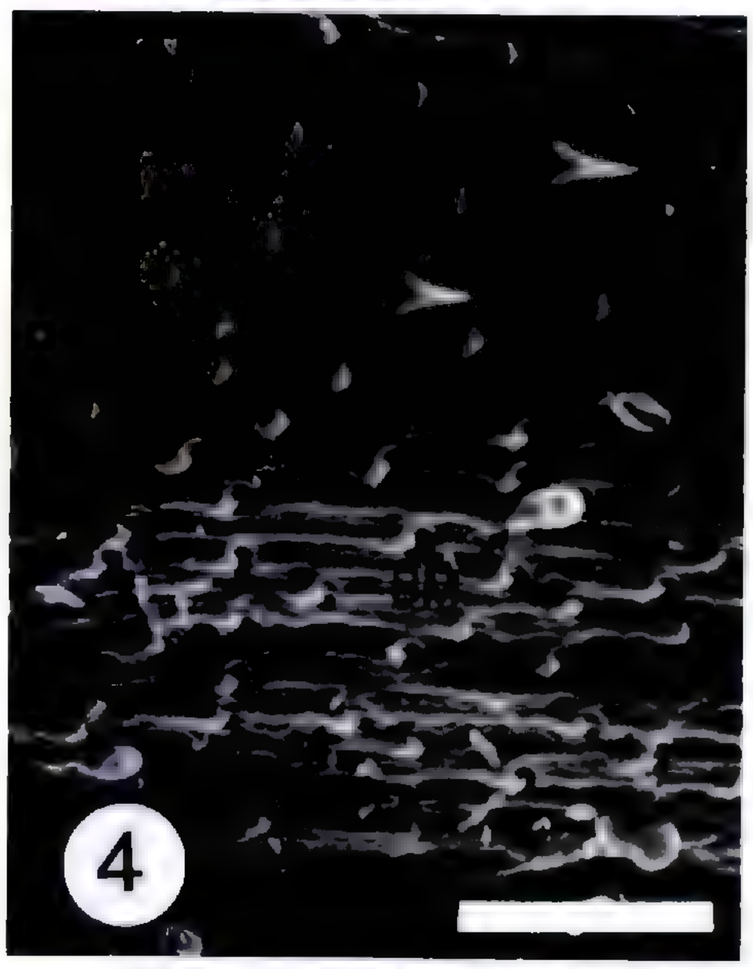
Viguierella madagascariensis A. Camus: *Gentry 11882*, Madagascar.

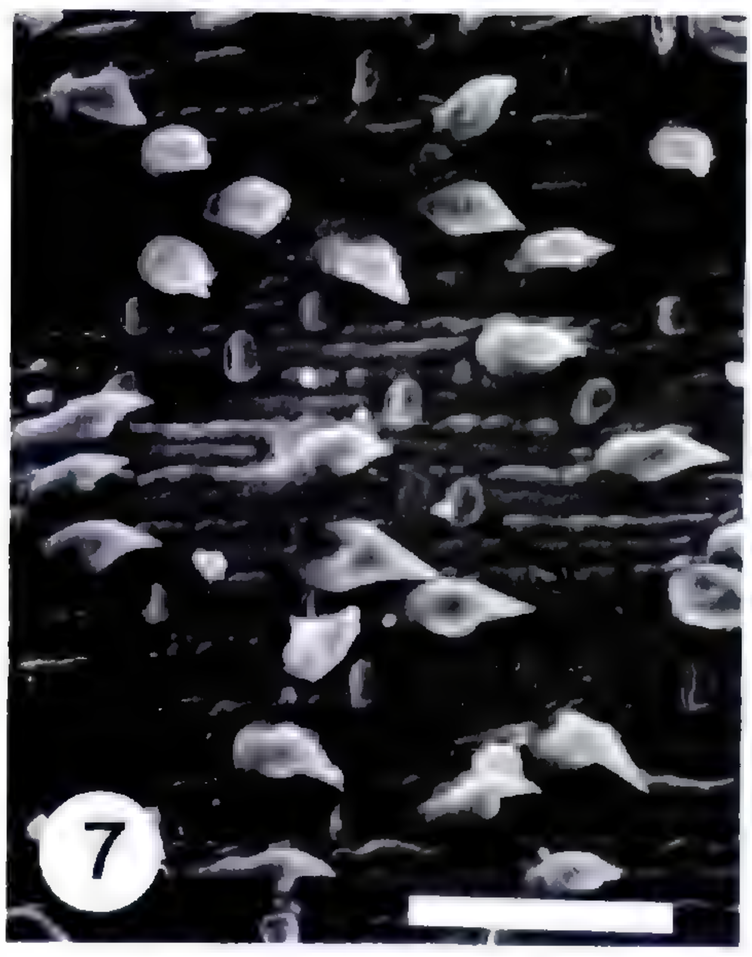
Note added in proof.

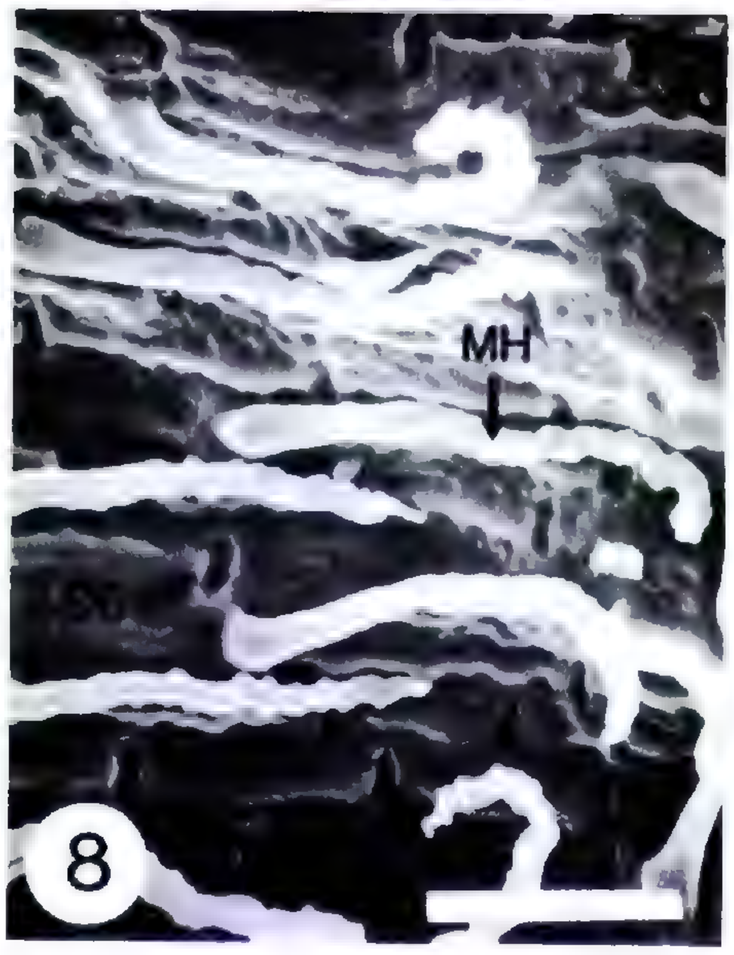
Re-examination of *Leptochloa obtusiflora* suggests some hairs on the lemma are clavate or clavicorniculate (*Mhoro 1868*; *Verdcourt 1101*; both at MO).

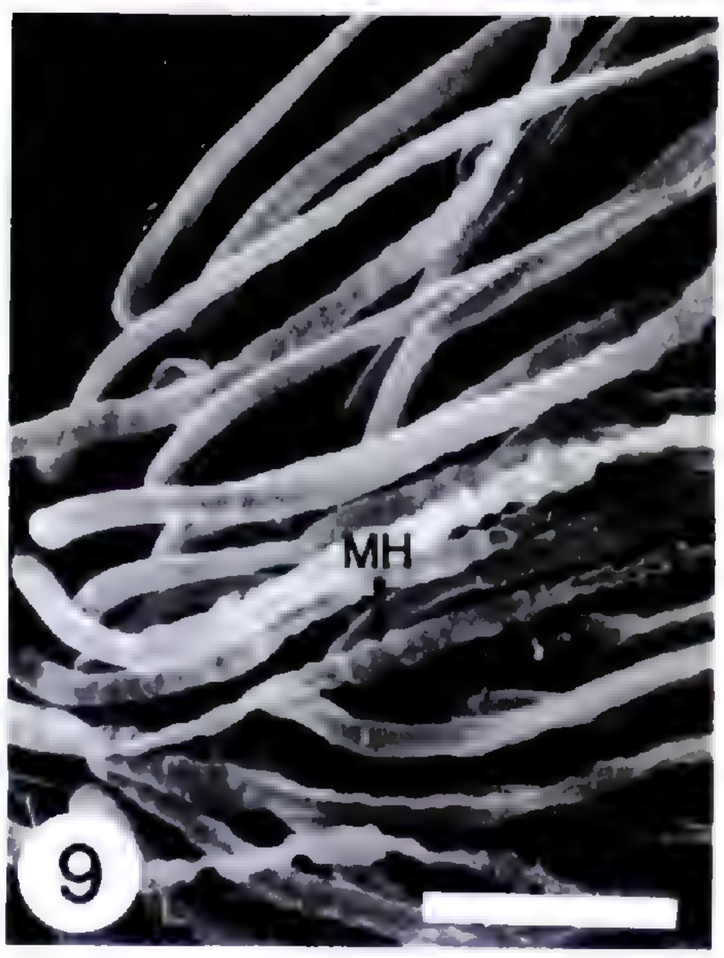






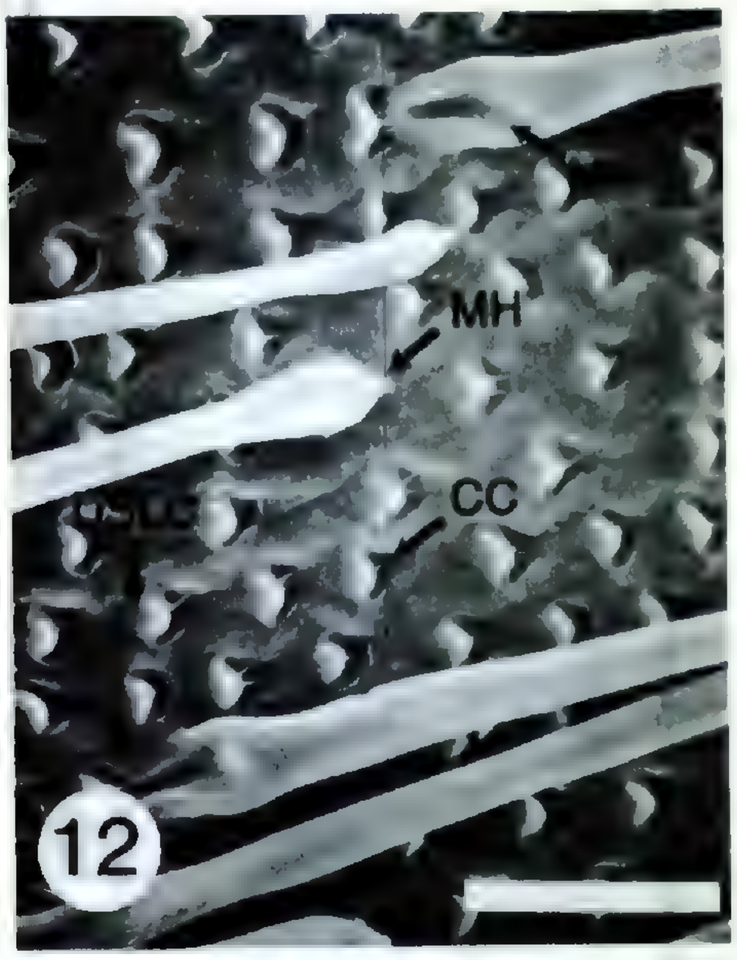


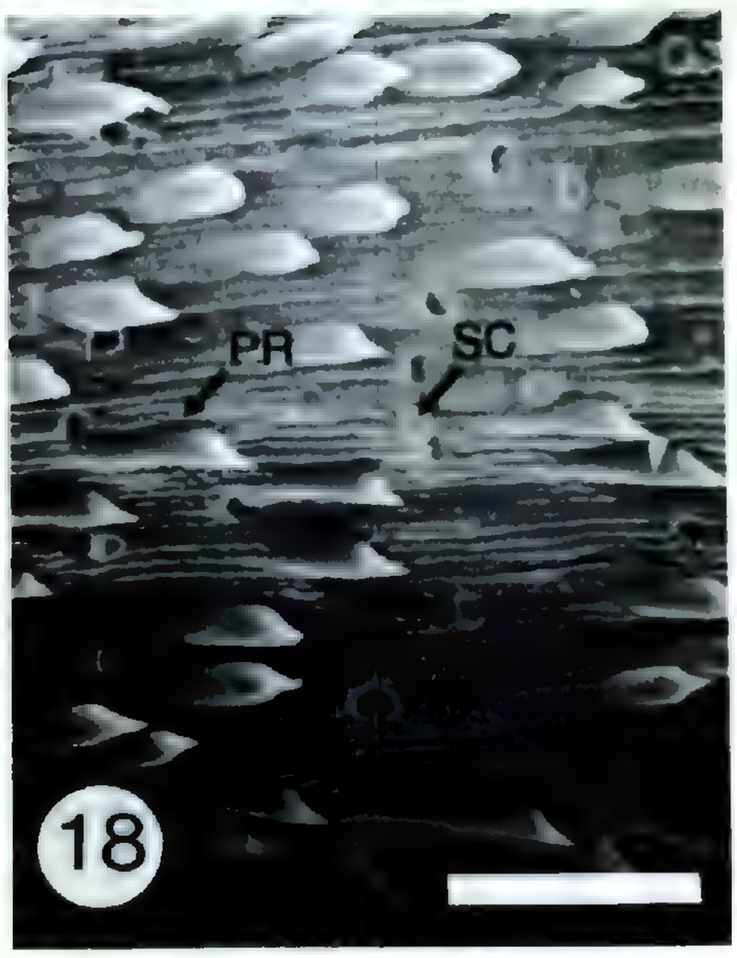




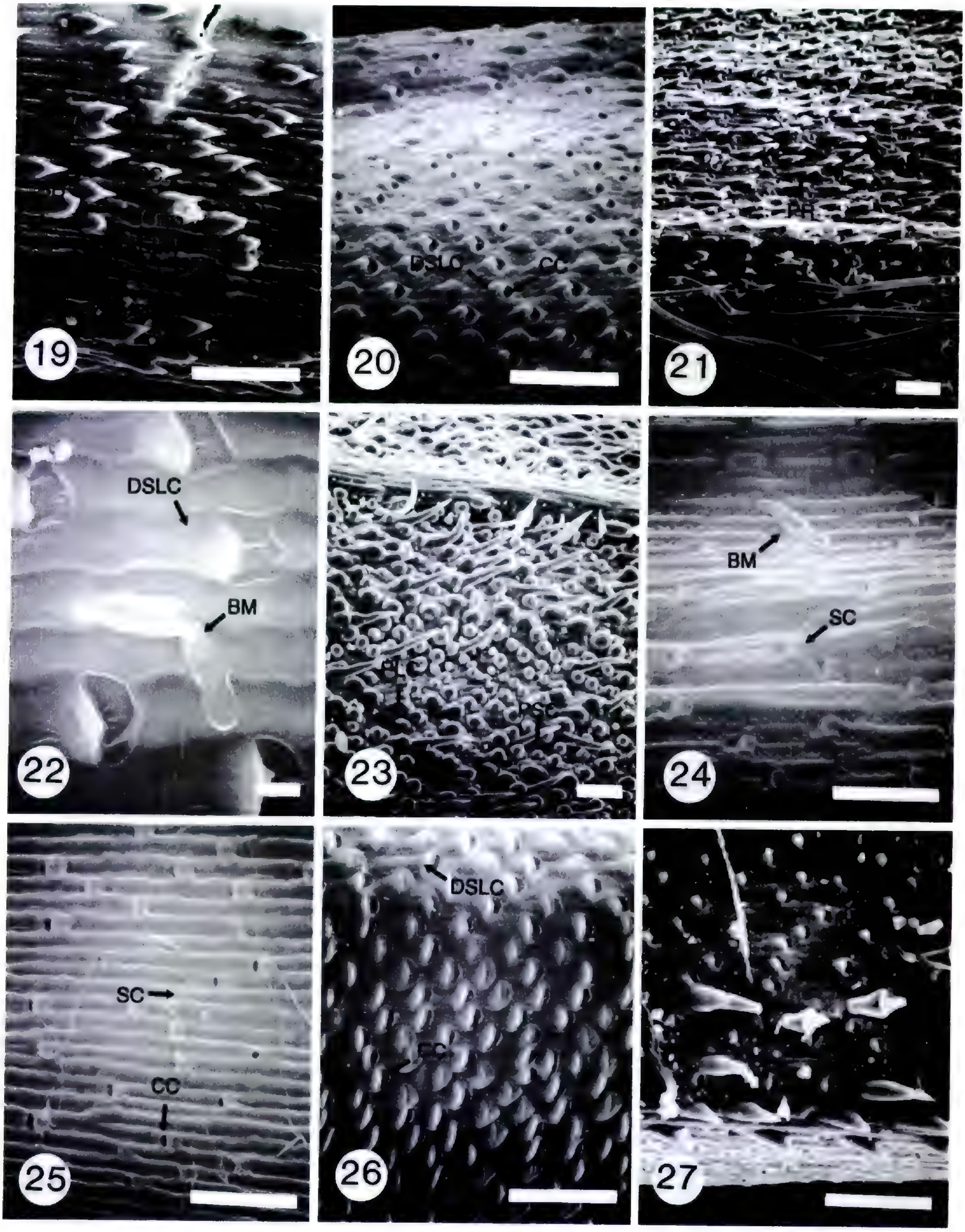
Figures 1–9.[3] —1. *Acracne racemosa*. —2. *Apochiton burttii*. —3. *Bewsia biflora*. —4. *Brachychloa schiemanniana*. —5. *Chloris verticillata*; from left to right, arrows illustrate sequential ontogeny of macrohair. —6. *Cladoraphis cyperoides*; bar = 5 μm. —7. *Cladoraphis spinosa*. —8. *Coelachyrum brevifolium*; note crispate macrohairs. —9. *Coelachyrum poiflorum*, with crispate macrohairs.

[3] Figures 1–72. SEM photomicrographs of lemmas of *Leptochloa* spp. and related genera. Unless indicated otherwise, scale bars equal 50 μm. Abbreviations: AELW = apical extensions of lateral walls of long cells; BM = bicellular microhair; CC = cork cell; DSLC = distally swelling long cell; MH = macrohair; PLC = papillate long cell; PR = prickle; PSC = papillate short cell; SC = silica cell. For details see text.

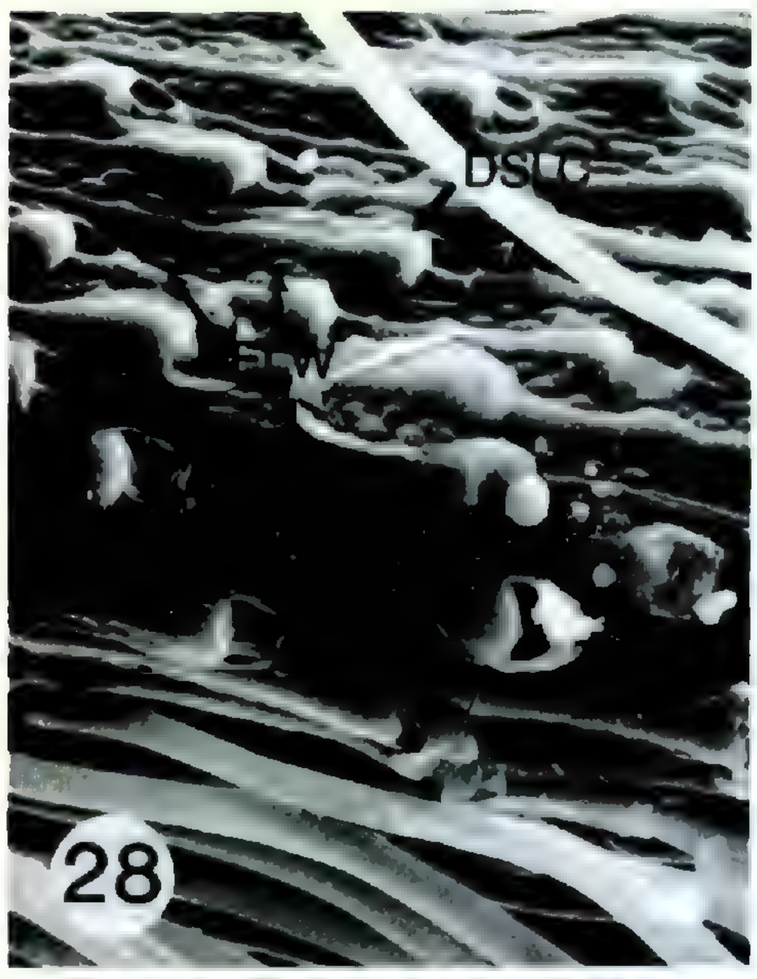


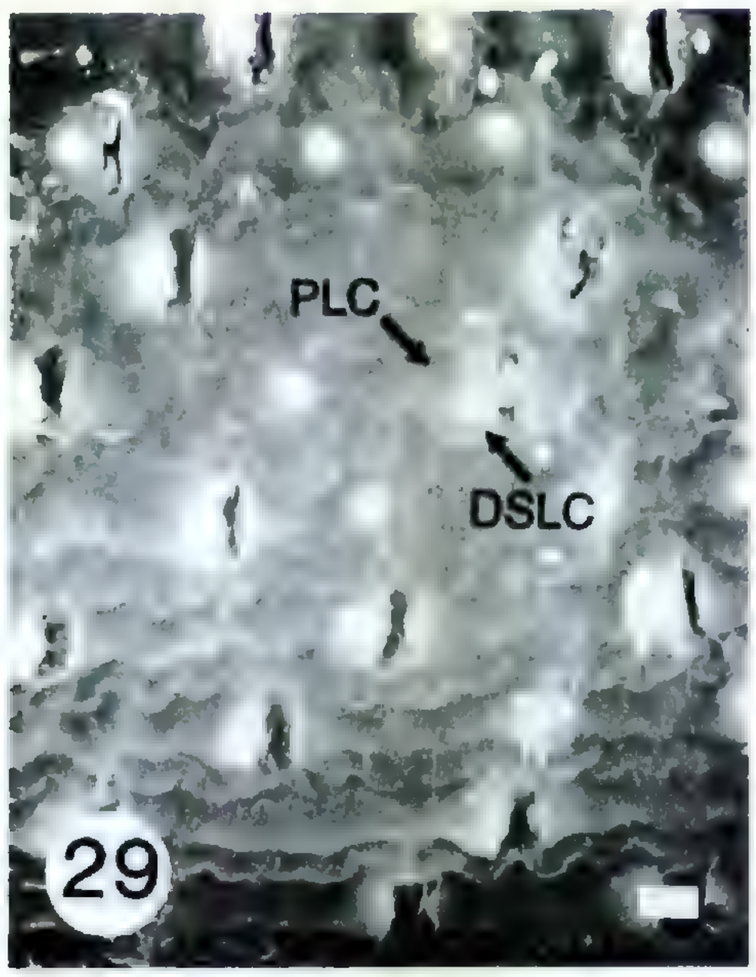


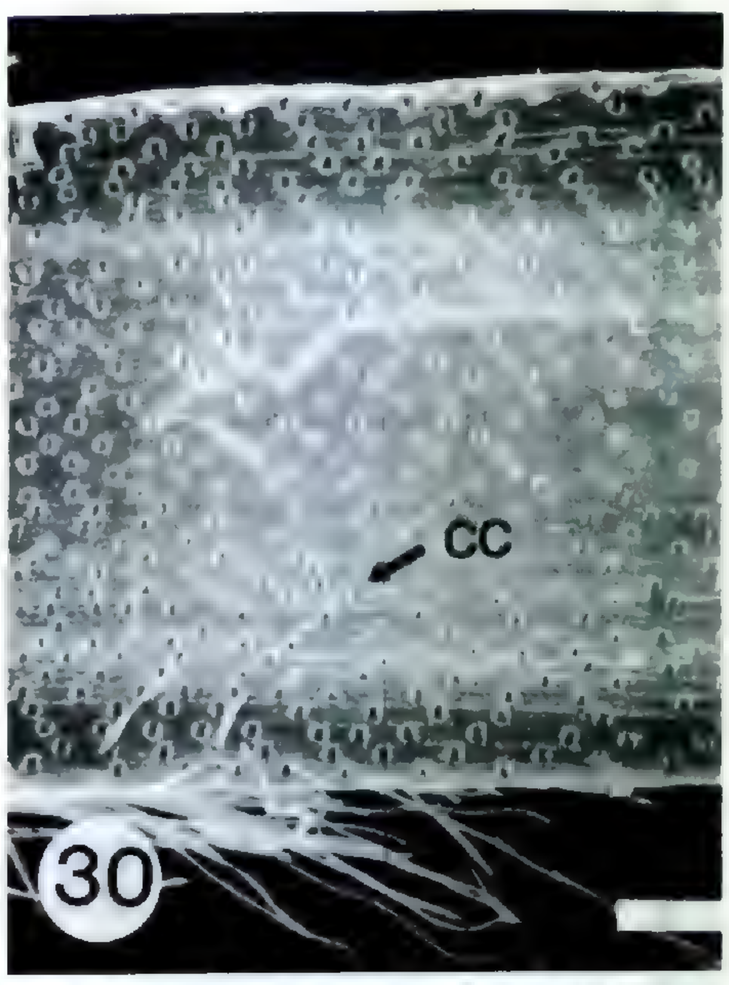
Figures 10–18.[3] —10. *Coelachyrum poiflorum*, note crispate macrohairs and non-swollen long cells; bar = 5 μm (lemmatal apex toward top). —11. *Coelachyrum stoloniferum*, with crispate macrohairs; bar = 5 μm. —12. *Coelachyrum yemenicum*, arrows indicate clavicorniculate apex of macrohairs and basally flattened and conduplicate macrohair bases. —13. *Cynodon nlemfuensis*, showing apiculate tips of macrohairs. —14. *Desmostachya bipinnata*. —15. *Dinebra retroflexa*. —16. *Drake-Brockmania somalensis*. —17. *Ectrosia gulliveri*. —18. *Ectrosia leporina*.

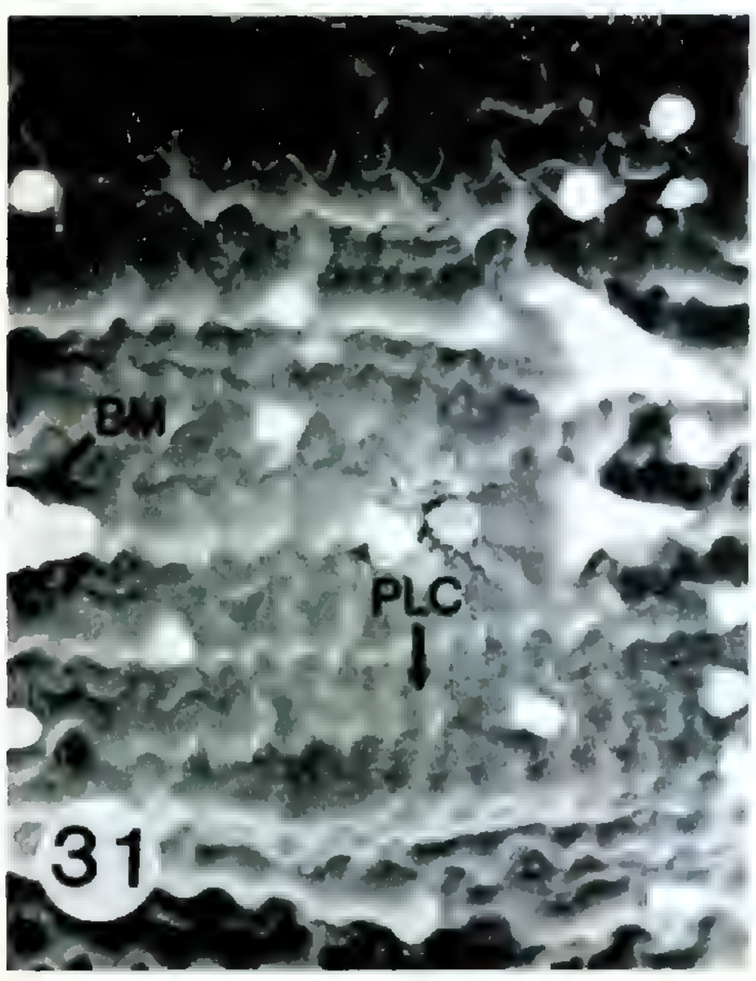


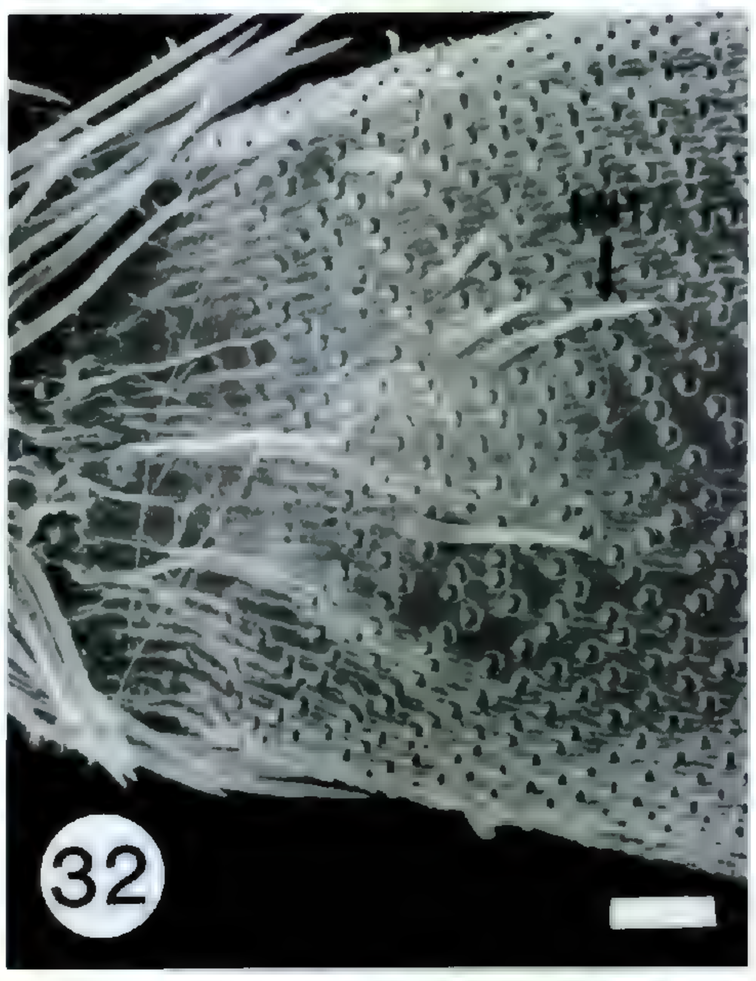
Figures 19–27.[3] —19. *Ectrosiopsis lasioclada*. —20. *Eragrostiella bifaria*; note swollen immature cork cells. —21. *Gouinia virgata*; prickles arising from long cells. —22. *Habrochloa bullockii*, panicoid microhair; bar = 5 μm. —23. *Halopyrum mucronatum*. —24. *Harpachne schimperi*. —25. *Heterachne abortiva*; bar = 5 μm. —26. *Indopoa pauperculata*; note swollen distal ends of long cells and swollen immature short cells; bar = 5 μm. —27. *Kengia serotina*.

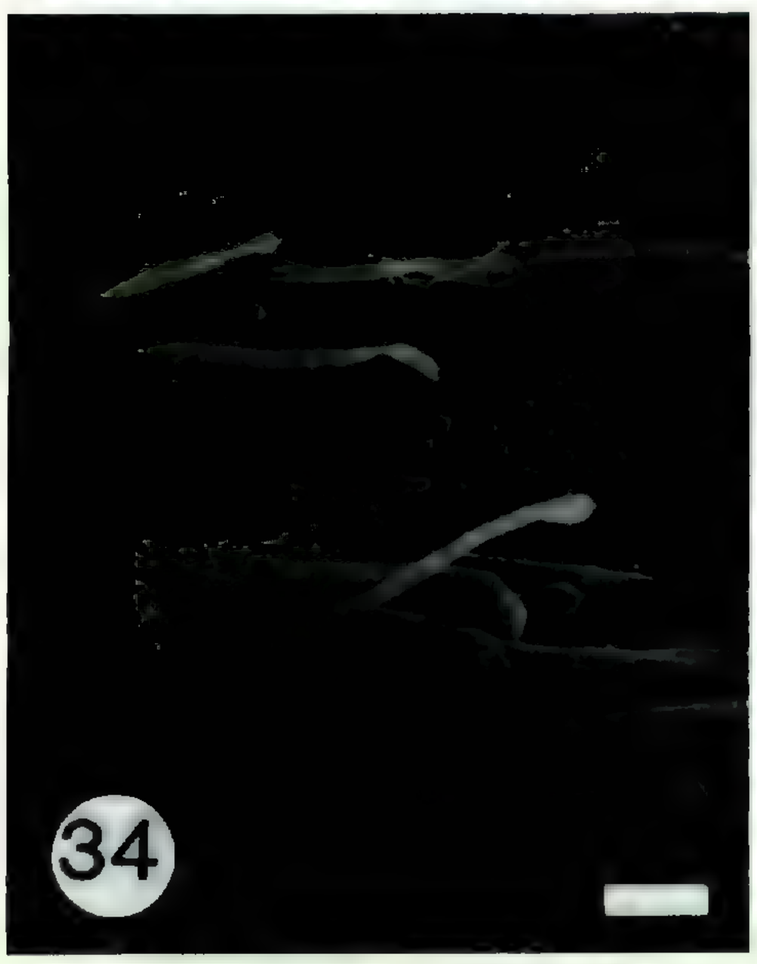


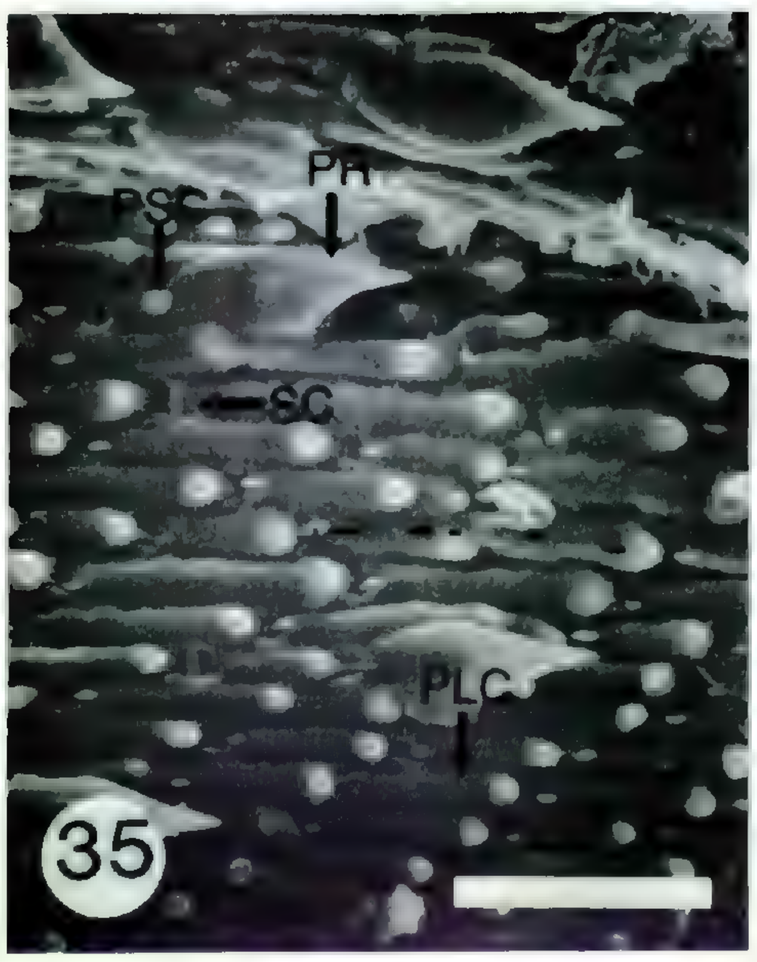




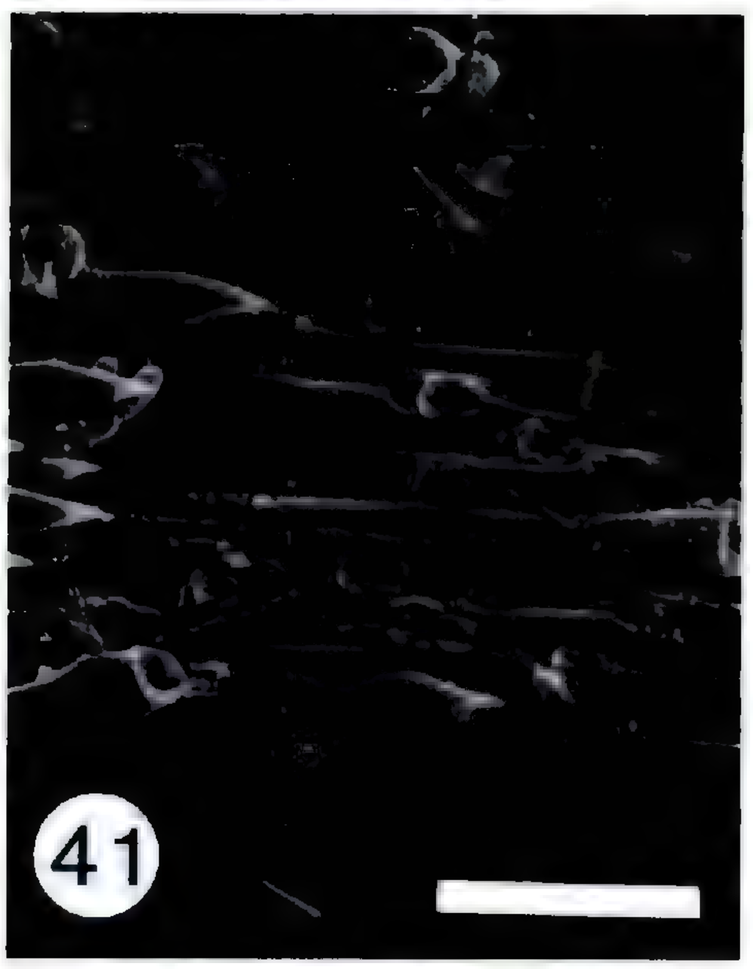


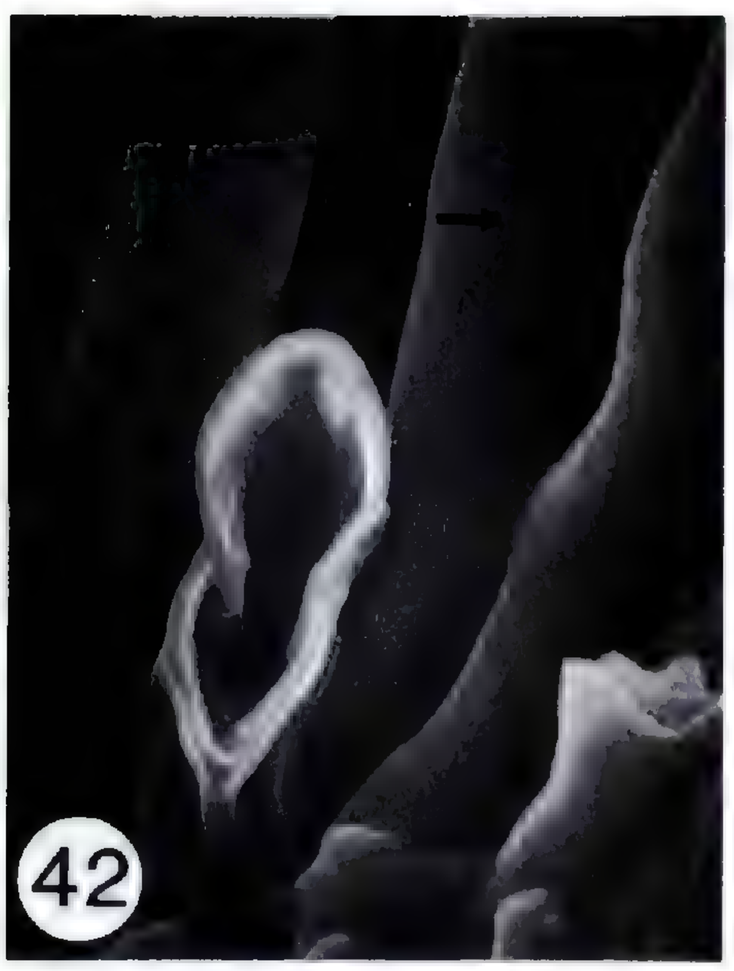


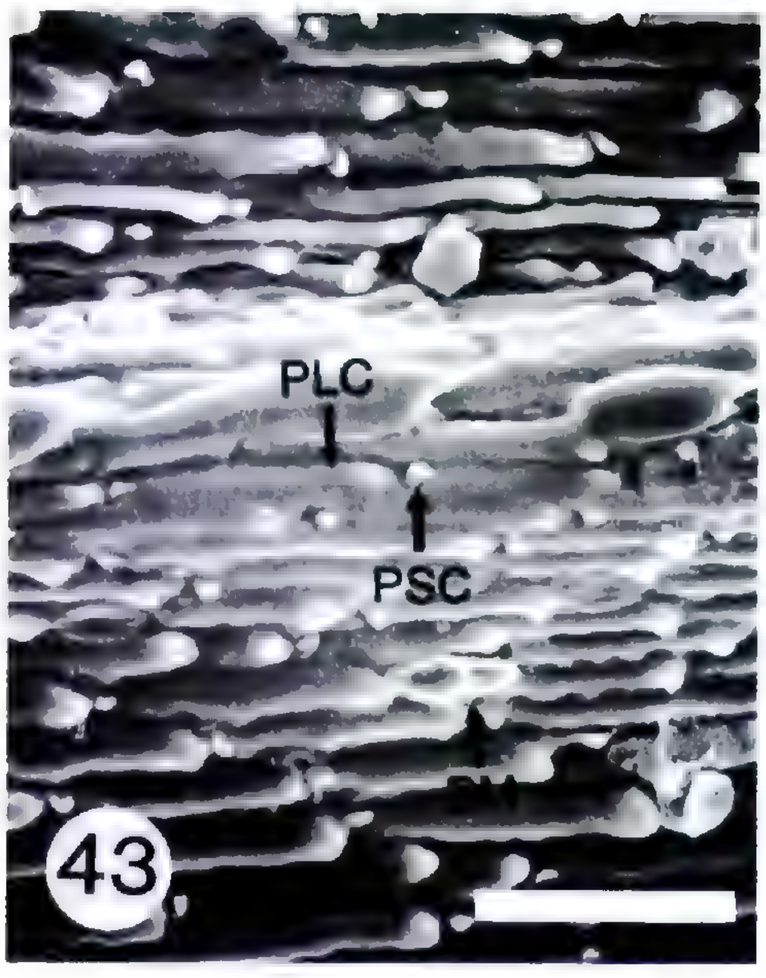


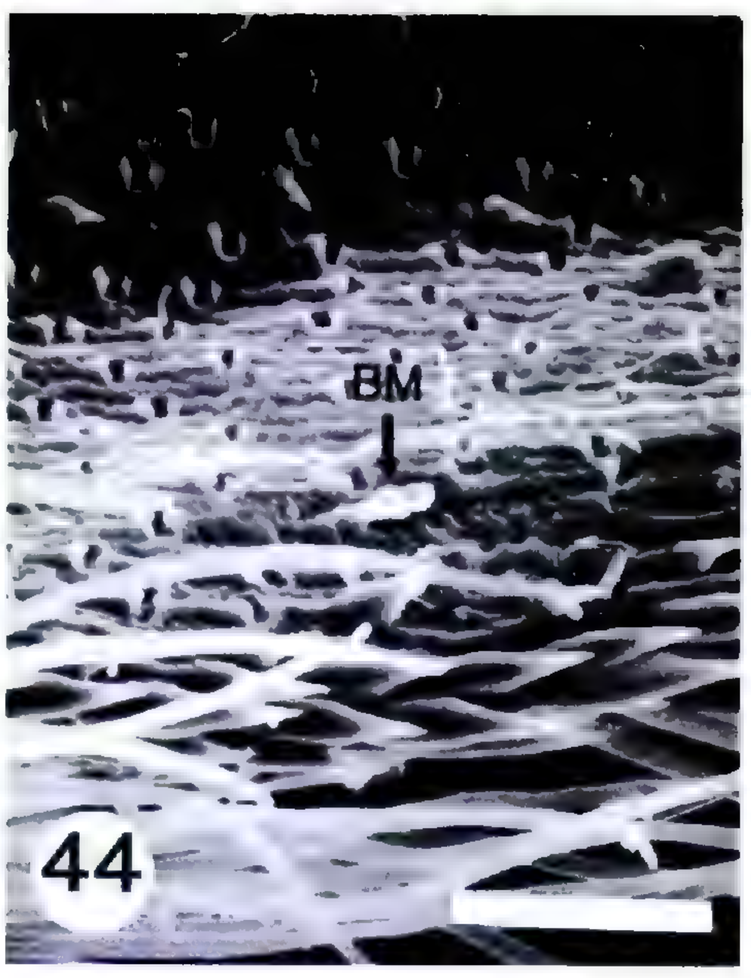


Figures 28–36.[3] —28. *Leptocarydion vulpiastrum*; note apical extensions of lateral walls along long cells; bar = 5 μm. —29. *Leptochloa chinensis*; note papillae occurring on distal swelling of long cell; bar = 5 μm. —30. *Leptochloa ciliolata*. —31. *Leptochloa coerulescens*; chloridoid microhair, papillate long cells, with relatively long papillae; bar = 5 μm. —32. *Leptochloa digitata*. —33. *Leptochloa dubia*. —34. *Diplachne eleusine*, with clavicorniculate macrohairs. —35. *Leptochloa fascicularis*, with a few sporadic silica cells. —36. *Leptochloa fascicularis*; macrohair arising from short cell.



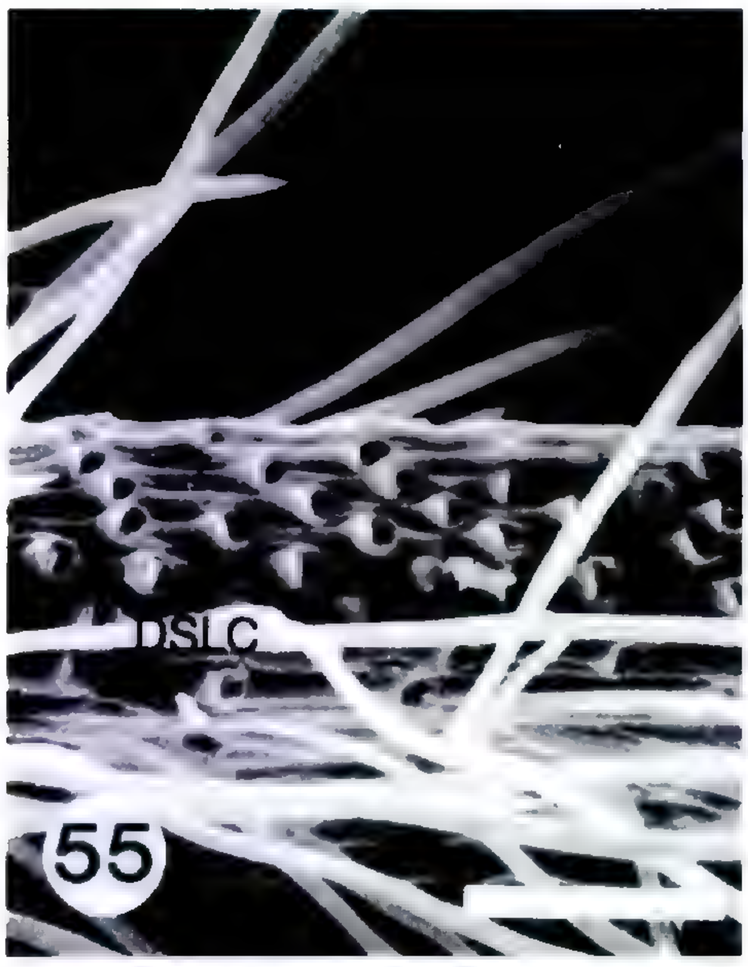


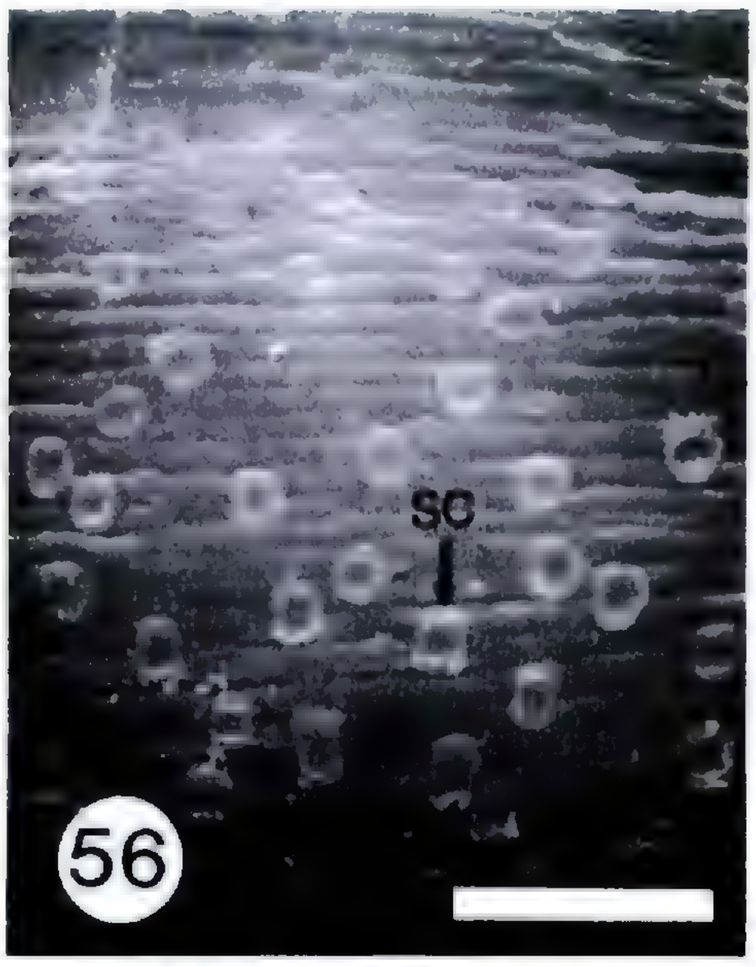


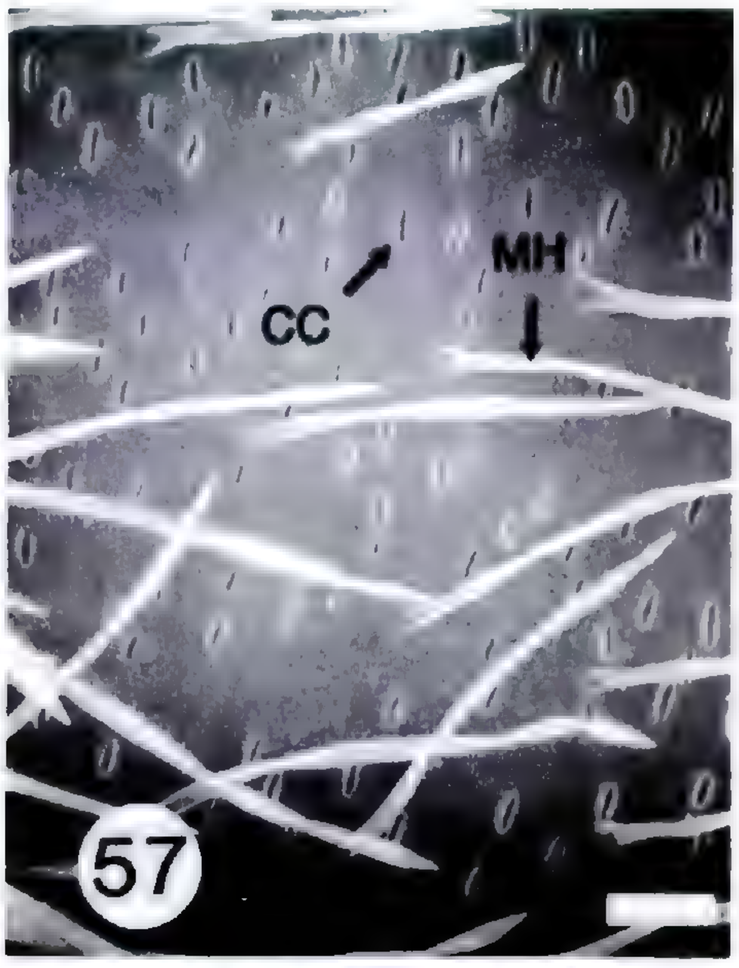


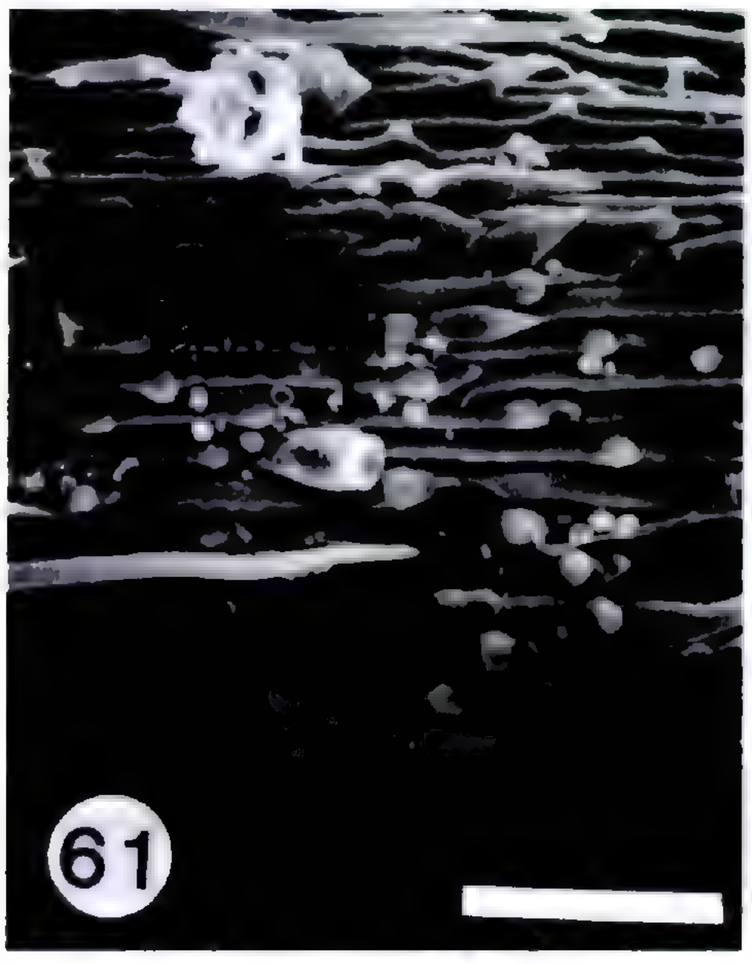
Figures 37–45.[3] —37. *Leptochloa fusca*; bar = 5 μm. —38. *Diplachne gigantea*, with prickles arising from short cells; bar = 5 μm. —39. *Leptochloa ligulata*. —40. *Leptochloa monticola*; note prickles arising from long cells and their conduplicate bases. —41. *Leptochloa monticola* with silica cells. —42. *Leptochloa mucronata*; macrohairs arising from distal end of long cells (lemmatal apex toward top). —43. *Diplachne muelleri*; papillate short and long cells. —44. *Leptochloa nealleyi*; note different prickle sizes. —45. *Leptochloa neesii*, with basally flattened macrohairs arising from short cells; bar = 5 μm.

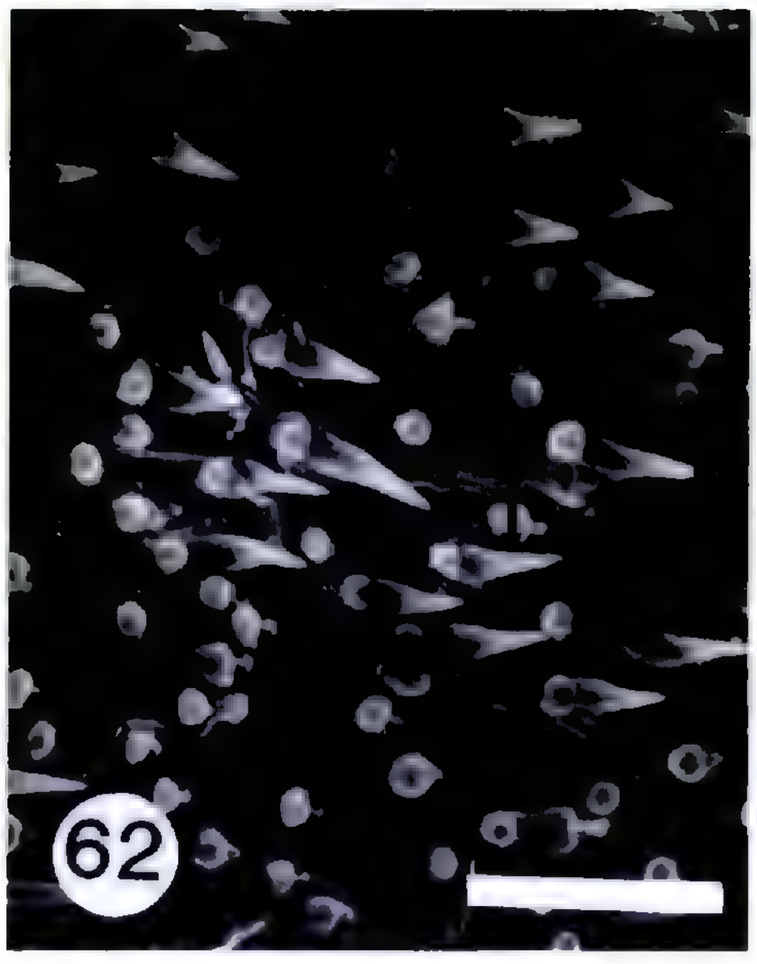
Figures 46–54.[3] —46. *Leptochloa panicea* with intercostal macrohairs. —47. *Leptochloa panicoides*; note thick basal cell of microhair. —48. *Leptochloa rupestris*. —49. *Leptochloa scabra*. —50. *Leptochloa squarrosa*; note basally flattened macrohair; bar = 5 μm. —51. *Leptochloa uniflora*; note atypically shortened long cells. —52. *Leptochloa virgata*, with swollen distal portions of long cells, and cork cells with collapsing outer walls. —53. *Leptochloa viscida*; note thick basal cell of microhair. —54. *Lintonia nutans*, with prickles arising at base of dorsal awn.

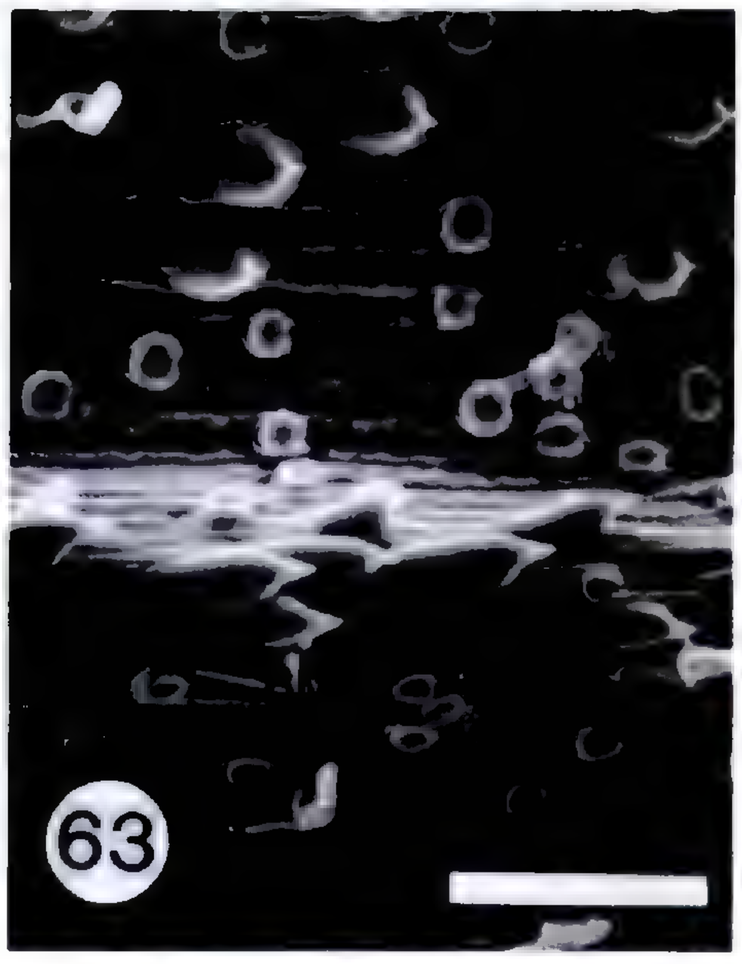




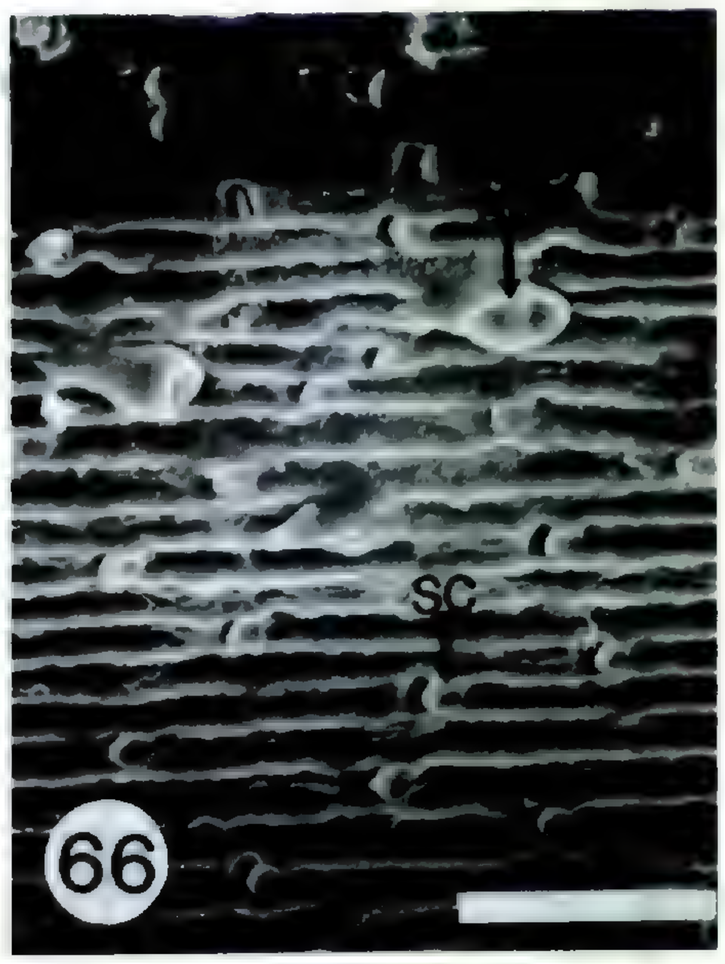


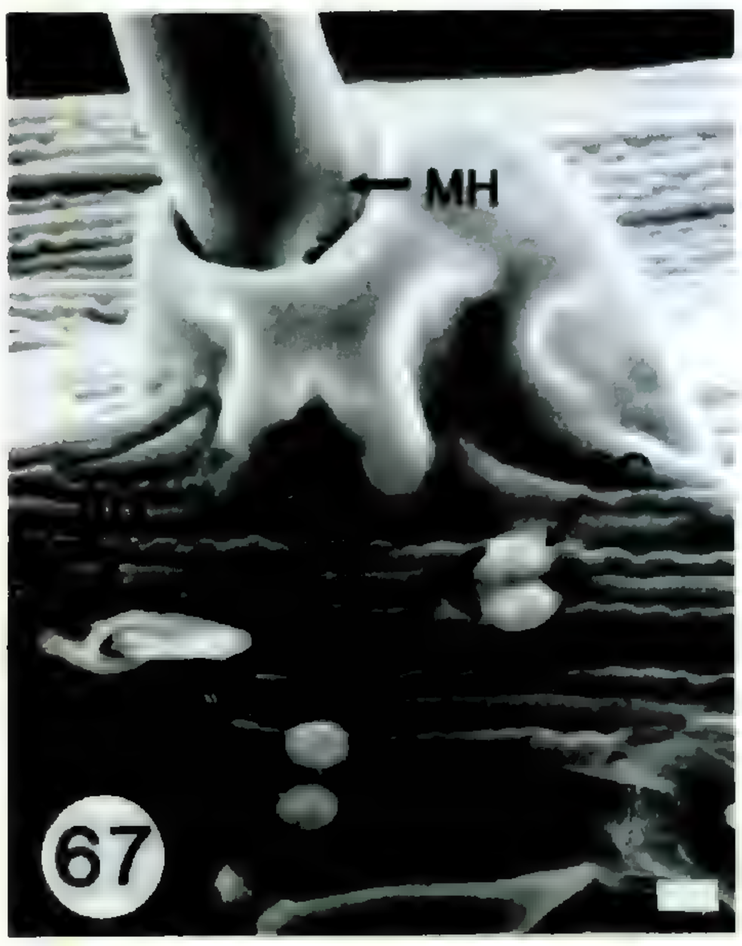


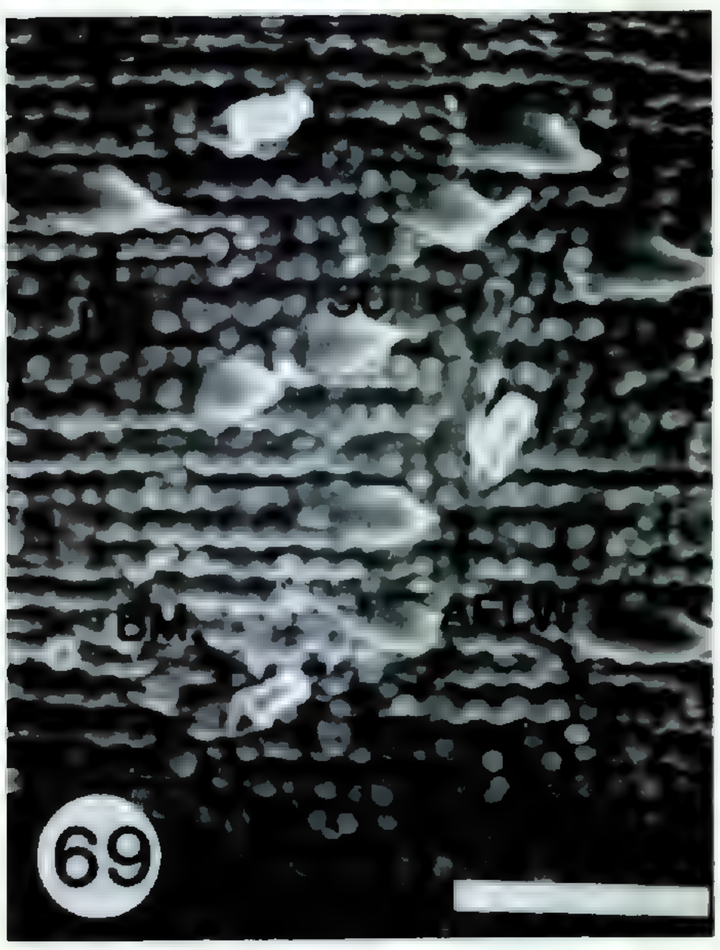


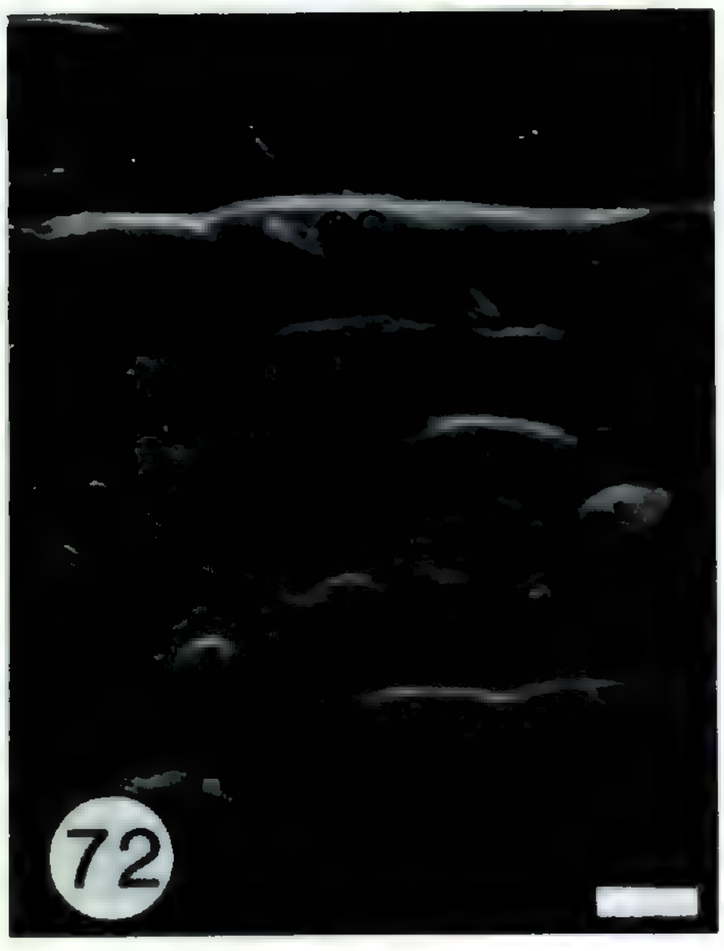


Figures 55–63.[1] —55. *Lophacme digitata*. —56. *Myriostachya wightiana*. —57. *Neesiochloa barbata*. —58. *Neyraudia reynauldiana* with panicoid microhair. —59. *Ochthochloa compressa*, showing hollow, basally severed macrohair; bar = 5 μm. —60. *Odyssea mucronata*; bar = 5 μm. —61. *Orinus thoroldii*. —62. *Oropetium aristatum*. —63. *Pogonarthria fleckii*; prickles arising from long cells and short cells.









Figures 64–72.[3] —64. *Pogoneura biflora*. —65. *Psammagrostis wiseana*; note enneapogonoid microhairs and swellings distal to the base of the microhair. —66. *Psilolemma jaegeri*. —67. *Richardsiella eruciformis* with papillate base of macrohair; bar = 5 μm. —68. *Sclerodactylon macrostachyum*. —69. *Steirachne barbata*; note apical extensions of lateral walls of long cells. —70. *Trichoneura grandiglumis*; note macrohairs with swollen bases (above) and macrohairs arising from the proximal end of long cells (below). —71. *Triraphis andropogonoides*. —72. *Viguierella madagascarensis*; bar = 5 μm.

FURTHER STUDIES ON PHORBOL ESTER BIOACTIVITY IN THE EUPHORBIACEAE[1]

John A. Beutler,[2] Ada Belinda Alvarado-Lindner,[3] and Thomas G. McCloud[3]

ABSTRACT

Six hundred and thirty-four organic extracts, including 36 previously untested genera of the Euphorbiaceae, were examined in a phorbol dibutyrate receptor binding assay. Phorbol bioactivity was newly detected in the genera *Anthostema, Blachia, Borneodendron, Dichostemma, Spirostachys, Tapoides, Trigonostemon,* and *Wetria.*

The activity of phorbol esters in the National Cancer Institute (NCI) primary anti-HIV screen (Gustafson et al., 1992; Erickson et al., 1995) prompted us to investigate the taxonomic distribution of phorbol esters, as measured by a simple competition binding assay. We have extended our previous study (Beutler et al., 1989) to detect the presence of phorbol esters in crude organic extracts of Euphorbiaceae. Our aim has been to examine as many tribes and genera as possible to map the distribution of phorbol ester bioactivity in the family.

MATERIALS AND METHODS

SAMPLES

The plant samples for this study were collected under the auspices of the NCI Developmental Therapeutics Program. Critical plant determinations were made by Michael Huft, Missouri Botanical Garden, D. Doel Soejarto, Field Museum, and John Burley, Arnold Arboretum. The taxonomic framework adopted was that of Webster (1994), except for the distinction of two species of *Wetria,* as maintained by Soejarto. Voucher specimens (see Appendix 1) are located at the Field Museum (Southeast Asia), the Missouri Botanical Garden (Africa), or the New York Botanical Garden (Americas) except where indicated in the appendix. Specimens without numbers (s.n.) are not vouchered. Dried plant materials were processed by percolation in a 1:1 mixture of methylene chloride:methanol, and the solvent evaporated in vacuo at 40°C. All crude extract samples were dissolved in DMSO at a concentration of 10–20 mg/ml for initial examination, then stored at −20°C. For dose response studies, these samples were further diluted in DMSO.

PHORBOL DIBUTYRATE BINDING ASSAY

The assay was performed as previously reported (Beutler et al., 1989). Each extract was tested at an initial concentration of 100 μg/ml. If displacement at this concentration was greater than 60 percent, it was taken as a positive result. The definition was increased from the value of 50 percent displacement used in our previous report, due to examination of nonspecific binding effects of the crude extracts. Initial examination and dose response were performed in duplicate, with at least four concentrations used for dose response. The incubation was terminated by filtration over Whatman GF/B glass fiber filters in a Brandel cell harvester. A recent modification of the assay used for a minority of samples involved a reduction of the assay volume to 250 μl in 96-well polypropylene microtiter plates, with harvest onto GF/B glass fiber paper, which was then dried *in vacuo* and counted on a Betaplate counter.

RESULTS AND DISCUSSION

The cumulative total of active genera including our previous results (Beutler et al., 1989) are tab-

[1] We thank the staff and collaborators of the NCI Developmental Therapeutics Program for their assistance, especially Gordon Cragg for management of the plant collection contracts, Michael J. Huft, D. Doel Soejarto, and John Burley for performing critical botanical determinations, and Peter M. Blumberg for helpful discussions. Research supported by the National Cancer Institute, DHHS, under contract with SAIC Frederick.

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Table 1. Distribution of phorbol bioactivity by genus (Webster, 1994), including previous results (Beutler et al., 1989).

Taxon	Samples active/ samples tested		
I. Phyllanthoideae			1/199
6. Antidesmeae		1/88	
Antidesma	1/42		
II. Oldfieldioideae			0/14
III. Acalyphoideae			4/169
30. Acalypheae		4/76	
Wetria	4/4		
IV. Crotonoideae			65/118
34. Manihoteae		1/3	
Cnidoscolus	1/2		
38. Jatropheae		8/8	
Jatropha	8/8		
39. Codiaeae		10/13	
Dimorphocalyx	2/2		
Codiaeum	6/6		
Blachia	2/2		
40. Trigonostemoneae		9/9	
Trigonostemon	9/9		
42. Croteneae		26/40	
Croton	23/37		
Eremocarpus	1/1		
Fahrenheitia	2/2		
44. Aleuritideae		11/21	
Aleurites	1/1		
Borneodendron	1/1		
Cyrtogonone	5/5		
Crotonogyne	2/2		
Tapoides	2/2		
V. Euphorbioideae			83/134
45. Stomatocalyceae		1/10	
Plagiostyles	1/3		
46. Hippomaninae		46/77	
Duvigneaudia	2/3		
Excoecaria	8/8		
Maprounea	5/8		
Omalanthus	6/15		
Sapium	19/25		
Spirostachys	4/5		
Stillingia	2/2		
49. Euphorbieae		36/47	
Anthostema	4/4		
Dichostemma	6/6		
Euphorbia	25/33		
Synadenium	1/1		

ulated (Table 1) according to Webster's (1994) arrangement of genera. Thirty-six genera that we had not previously examined were tested (*Amanoa, Anthostema, Austrobuxus, Blachia, Borneodendron, Cephalomappa, Chaetocarpus, Chamaesyce, Cleidion, Clutia, Conceveiba, Dichostemma, Elateriospermum, Erythrococca, Koilodepas, Lingelsheimia, Monadenium, Neoscortechinia, Omphalea, Pausandra, Pera, Pimelodendron, Plukenetia, Pseudolachnostylis, Ptychopyxis, Sampantaea, Sauropus, Savia, Sebastiania, Senefeldera, Strophioblachia, Synadenium, Tapoides, Trigonostemon, Wetria,* and *Zimmermanniopsis*), bringing the total number of genera tested to 111. Further species and plant parts of previously tested genera were also examined. Representatives of a total of 39 of the 49 tribes distinguished (Webster, 1994) have been examined. In total, 106 species in the subfamily Phyllanthoideae, and 2 species of the Oldfieldioideae have been examined with negative results. A single positive test of *Antidesma nigricans* Tul. (Phyllanthoideae) seeds (Beutler et al., 1989) prompted us to test a sample from each of the 26 species of *Antidesma* in the NCI repository. The lack of further positive results with these samples leads us to suspect that the single positive sample may have been misidentified. Seventy-six species of Acalyphoideae were tested, with 2 species of *Wetria* being positive (see below). Thirty-two of the 51 species of Crotonoideae examined appear to contain phorbol esters (63%), while 43 of the 63 species of Euphorbioideae tested are active (68%).

While the results of the ^{3}H-PDBu binding assay reflect only the presence of phorbol esters which bind to protein kinase C, there appears to be a good correlation between the bioactivity data and the chemical literature on phorbol diterpene distribution. Our laboratory has demonstrated in three specific instances (*Homalanthus nutans* (Forster) Pax (Gustafson et al., 1992), *Excoecaria agallocha* L. (Erickson et al., 1995), and *Maprounea* spp. (Beutler et al., 1995)) that the activity detected in our samples is due to conventional phorbol esters. Isolation of the compounds responsible for ^{3}H-PDBu binding activity in the newly identified genera (*Anthostema, Blachia, Borneodendron, Dichostemma, Spirostachys, Tapoides, Trigonostemon,* and *Wetria*) should be pursued to positively identify the compounds responsible for the observed bioactivity.

These results indicate that phorbol ester bioactivity is primarily limited to subfamilies IV and V in Webster's (1994) scheme. The only exception found in our data is that for two species of *Wetria,* which is placed in the Acalyphoideae. The overall pattern of distribution is consistent with previous chemotaxonomic data (Kinghorn, 1979) and lends biochemical support to Webster's arrangement of genera. Further, our data are consistent with embryological data (Jensen et al., 1994), and legumin-like protein distribution (Kapil & Bhatnagar, 1994),

which both separate the Phyllanthoideae and Oldfieldioideae from the other three subfamilies.

The observation of ^{3}H-PDBu binding activity in *Wetria insignis* and *W. macrophylla*, and the isolation of phorbol esters from *Pycnocoma* by Bergquist et al. (1989) may appear anomalous, but would be consistent with the proposed derivation of Crotonoideae and Euphorbioideae from Acalyphoideae if the biosynthetic capability to form phorbol esters arose in a common ancestor of the Acalyphoideae, Crotonoideae, and Euphorbioideae. Hecker and Adolf have perceived a similar chemotaxonomic pattern to that which we observed (Adolf & Hecker, 1977). It must be emphasized that no definitive work has been done on the biosynthesis of any phorbol ester in any plant. Such a study would facilitate interpretation of the chemical data for taxonomic or phylogenetic purposes. Alternative explanations for our pattern of results are that *Wetria* and *Pycnocoma* have been misclassified or misidentified; however, we believe the identifications to be correct. It is notable, however, that *Wetria* and *Pycnocoma* are placed in different tribes, and that their close relatives such as *Cleidion* or *Sampantaea*, and *Ptychopyxis*, respectively, have not displayed ^{3}H-PDBu displacing activity.

Patterns of diterpene occurrence and irritancy have been previously examined by Schmidt (1986), who analyzed the occurrence of all diterpene hydrocarbon skeletons (e.g., crotofolane, lathyrane, casbane, etc.) in the Euphorbiaceae. Since that review, other novel diterpene skeletal types have been discovered, and known types have been found in previously unexamined genera (e.g., Kashman et al., 1993; Bernart et al., 1993).

We conclude that phorbol bioactivity and phorbol ester biosynthesis are more widespread throughout the genera of the Euphorbiaceae than has been previously reported. The chemotaxonomy of this family can be explored by application of the ^{3}H-PDBu binding method to more taxa, and by bioassay-guided fractionation to determine the chemical structures responsible for these results. The ^{3}H-PDBu binding assay allows rapid testing, generating semiquantitative data that can be used to prioritize isolation of the compounds responsible for the bioactivity. It is more selective than such assays as mouse ear irritancy and does not require the use of whole animals. The distribution of ^{3}H-PDBu binding activity may also be of use in assessing the potential toxicology of Euphorbiaceae used as phytomedicines.

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Appendix 1. Specimens of Euphorbiaceae examined. The characters + and − refer to the ^{3}H-PDBu screening results for the specimen.

Acalypha lancetillae Standley, *Balick 1924* (NY) (−); *Alchornea cordifolia* (Schum. & Thonn.) Muell. Arg., *Fay 8575* (MO) (−); *Amanoa bracteosa* Planch., *Jongkind 2147* (MO) (−); *Amanoa caribaea* Krug & Urb., *Tuxill 106* (NY) (−); *Amanoa strobilacea* Muell. Arg., *McPherson 15094* (MO) (−); *Anthostema aubryanum* Baillon, *McPherson 15212, Wilks 2626* (MO) (+); *Antidesma bunius* (L.) Spreng., *Burley 68* (F) (−); *Antidesma celebicum* Miq., *Burley 3558* (F) (−); *Antidesma coriaceum* Tul., *Soepadmo 318* (F) (−); *Antidesma cumingii* Muell. Arg., *Soejarto 7375* (F) (−); *Antidesma cuspidatum* Muell. Arg., *Soepadmo 110* (F) (−); *Antidesma ghaesembilla* Gaertn., *Varadarajan 1528* (F) (−); *Antidesma gymnogyne* Pax & K. Hoffm., *Soejarto 5878* (F) (−); *Antidesma leptocladum* Tul., *Burley 173* (F) (−); *Antidesma leucocladum* Hook. f.,

Soepadmo 111 (F) (−); *Antidesma leucopodum* Miq., *Soepadmo 96* (F) (−); *Antidesma luzonicum* Merr., *Soejarto 7790* (F) (−); *Antidesma membranaceum* Muell. Arg., *Schmidt 1137* (MO) (−); *Antidesma menasu* Miq., *Bhaduri 35* (a) (−); *Antidesma montanum* Bl., *Soepadmo 59* (F) (−); *Antidesma neurocarpum* Miq., *Burley 371* (F) (−); *Antidesma nitidum* Tul., *Varadarajan 1501* (F) (−); *Antidesma pendulum* Hook. f., *Soepadmo 210* (F) (−); *Antidesma pentandrum* (Blanco) Merr., *Soejarto 7937* (F) (−); *Antidesma petiolare* Tul., *Miller 3741* (MO) (−); *Antidesma petiolatum* Airy Shaw, *Takeuchi 4444* (F) (−); *Antidesma polyanthum* K. Schum. & Laut., *Takeuchi 4388* (F) (−); *Antidesma salicinum* Ridl., *Soepadmo 261, Ong 172* (F) (−); *Antidesma sarcocarpum* Airy Shaw, *Takeuchi 7048* (F) (−); *Antidesma tomentosum* Bl., *Burley 53* (F) (−); *Antidesma venosum* Tul., *Schmidt 1236* (MO) (−); *Aporusa arborea* (Bl.) Muell. Arg., *Burley 1727* (F) (−); *Aporusa planchoniana* Baill., *Soejarto 5950* (F) (−); *Aporusa prainiana* King ex Gage, *Burley 1722* (F) (−); *Austrobuxus nitidus* Miq., *McDonald 4055, Burley 4589* (F) (−).

Baccaurea puberula Merr., *Meijer 122596* (F) (−); *Bischofia javanica* Bl., *Soejarto 5842* (F) (−); *Borneodendron aenigmaticum* Airy Shaw, *Meijer 109845* (F) (+).

Cephalomappa sp., *Frodin 2069* (F) (−); *Chaetocarpus castanicarpus* (Roxb.) Thw., *Soepadmo 308* (F) (−); *Chaetocarpus globosus* (Sw.) Fawc. & Rend., *Zanoni 45133, Garcia 2635* (NY) (−); *Chrozophora* sp., *Ghafoor 4510* (F) (−); *Claoxylon longifolium* (Bl.) Miq., *Burley 382* (F) (−); *Cleidion lanceolatum* Merr., *Soejarto 7975* (F) (−); *Cleidion spiciflorum* (Burm. f.) Merr., *Soejarto 7797* (F) (−); *Cleistanthus insignis* Airy Shaw, *Takeuchi 4634* (F) (−); *Clutia abyssinica* Jaub. & Spach, *Gereau 3027* (MO) (−); *Codiaeum luzonicum* Merr., *Soejarto 6195* (F) (+); *Codiaeum variegatum* (L.) A. Juss., *Harini 135* (F) (+); *Conceveiba rhytidocarpa* Muell. Arg., *Beck 1049* (NY) (−); *Croton argyratus* Bl., *Soejarto 6190, Burley 1468* (F) (+); *Croton lechleri* Muell. Arg., *Boom 7792, Bennett 4531* (NY) (+); *Croton leiophyllus* Muell. Arg., *Soejarto 6455* (F) (+); *Croton macrostachyus* Del., *Gereau 2576* (MO) (+); *Croton monathgynus* Michx., *Spjut 11129* (b) (−); *Croton palawanensis* Merr., *Soejarto 6476* (F) (+); *Croton punctatus* Jacq., *Beutler s.n.* (+); *Croton* spp., *Daly 5617* (+), *Williams 656* (+), *Takeuchi 4508* (−) (F); *Cyrtogonone argentea* (Pax) Prain, *McPherson 13735* (MO) (+).

Dichostemma glaucescens Pierre, *McPherson 15198, Dibata 935* (MO) (+); *Drypetes longifolia* (Bl.) Pax & K. Hoffm., *Burley 755* (F) (−); *Drypetes madagascariensis* (Lam.) Humbert & Leandri, *Zarucchi 7459* (MO) (−); *Drypetes parvifolia* (Muell. Arg.) Pax & K. Hoffm., *Fay 8260* (MO) (−); *Drypetes paxii* Hutch., *Martin 509* (MO) (−); *Drypetes sibuyanensis* (Elmer) Pax & K. Hoffm., *Burley 3029* (F) (−); *Drypetes similis* Hutch., *Nemba 551* (MO) (−).

Elateriospermum tapos Bl., *Burley 3175, Soepadmo 193, Frodin 2022* (F) (−); *Endospermum diadenum* (Miq.) Airy Shaw, *Burley 1450* (F) (−); *Erythrococca ulugurensis* A. R.-Sm., *Gereau 2949* (MO) (−); *Euphorbia laurifolia* Juss., *Mena 61* (NY) (+); *Euphorbia maculata* L., *Beutler s.n.* (−); *Euphorbia tirucalli* L., *Harini 150* (F) (+); *Excoecaria phillipensis* Merr., *Soejarto 6553* (F) (+).

Flueggea virosa (Willd.) Voigt, *Rulangaranga 7* (MO) (−).

Glochidion pomiferum Airy Shaw, *Takeuchi 4076* (F) (−).

Homonoia riparia Lour., *Ong 170* (F) (−); *Hyeronima clusioides* (Tul.) Muell. Arg. *Acevedo 2163* (NY) (−).

Koilodepas brevipes Merr., *Burley 707* (F) (−).

Lingelsheimia frutescens Pax, *McPherson 15084* (MO) (−).

Macaranga conifera (Zoll.) Muell. Arg., *Meijer 119104* (F) (−); *Macaranga denticulata* (Bl.) Muell. Arg., *Stone 15911* (F) (−); *Macaranga lowii* King ex Hook. f., *Burley 1397* (F) (−); *Macaranga pleioneura* Airy Shaw var. *velutina* Whitmore, *Takeuchi 4499* (F) (−); *Macaranga ramiflora* Elm., *Stone 15849* (F) (−); *Mallotus cuneatus* Ridl., *Soejarto 5791* (F) (−); *Mallotus philippinensis* (Lam.) Muell. Arg., *Soejarto 6230* (F) (−); *Mallotus ricinoides* (Pers.) Muell. Arg., *Burley 79* (F) (−); *Margaritaria discoidea* (Baill.) Webster, *Gereau 2574* (MO) (−); *Monadenium laeve* Stapf., *Kayombo 1027* (MO) (−).

Neoschortechinia kingii (Hook. f.) Pax & K. Hoffm., *Burley 1380* (F) (−); *Neoschortechinia nicobarina* Hook. f., *Burley 2478* (F) (−); *Neotrewia cumingii* (Muell. Arg.) Pax & K. Hoffm., *Madulid 6798, Burley 3587* (F) (−).

Omalanthus acuminatus (Muell. Arg.) Pax, *Cox 1021* (BRY) (+); *Omalanthus megaphyllus* Merr., *Nicholson 1* (c) (+); *Omalanthus nervosus* J. J. Sm., *Takeuchi 4176* (F) (−); *Omalanthus novaguinensis* (Warb.) K. Sch., *Takeuchi 4004* (F) (−); *Omalanthus leschenaultianus* A. Juss., *Nicholson 3* (c) (+); *Omalanthus rotundifolius* Merr., *Nicholson 4* (c) (−).

Pausandra sp., *Daly 6034* (MO) (−); *Pera arborea* Mutis, *Balick 3036, Balick 3066* (NY) (−); *Pera benesis* Rusby, *Betella 109* (NY) (−); *Pimelodendron amboinicum* Hassk., *Takeuchi 4236* (F) (−); *Plukenetia* sp., *Acevedo 1691* (NY) (−); *Pseudolachnostylis maprouneifolia* Pax var. *maprouneifolia, Gereau 2749* (MO) (−); *Ptychopyxis philippina* Croiz., *McDonald 3745* (F) (−).

Sampantaea amentiflora Airy Shaw, *Soejarto 8202* (F) (−); *Sapium biloculare* (S. Wats.) Pax, *Wirt s.n.* (d) (+); *Sapium laurocerasus* Desf., *Acevedo 2181* (NY) (+); *Sapium marmieri* Huber, *Daly 5634* (MO) (+); *Sapium* sp., *Soejarto 6193* (F) (+); *Sauropus androgynous* Merr., *Harini 35* (F) (−); *Savia platyrhachis* Baill., *Harder 1620* (MO) (−); *Sebastiania brasiliensis* Spreng., *Saldias 745* (NY) (−); *Securinega virosa* (Roxb.) Baill., *Fay 8060* (MO) (−); *Senefeldera* cf. *macrophylla* Ducke, *Beck 1056* (NY) (−); *Spirostachys africana* Sond., *Muhoro 6252* (MO) (+); *Stillingia sylvatica* L., *Spjut s.n.* (b) (+); *Strophioblachia fimbricalyx* Boerl., *Soejarto 6321* (F) (−); *Synadenium glaucescens* Pax, *Rulangaranga 179* (MO) (+).

Tapoides villamilii (Merr.) Airy Shaw, *Meijer 128772* (F) (+); *Thecacoris madagascariensis* A. Juss. var. *montana* Leandri, *Zarucchi 7384* (MO) (−); *Trigonostemon sumatranus* Pax & K. Hoffm., *Burley 689* (F) (+); *Trigonostemon viridissimus* (Kurz) Airy Shaw, *McDonald 3401* (F) (+).

Wetria insignis (Steud.) Airy Shaw, *Takeuchi 6386* (F) (+); *Wetria macrophylla* (Bl.) J. J. Sm., *Soejarto 7770* (F) (+).

Zimmermanniopsis uzungwae A. R.-Smith (ined.), *Kayombo 610* (MO) (−).

(a) Voucher: Central Drug Research Institute, Lucknow, India.

(b) Voucher: World Botanical Associates, Laurel, Maryland, U.S.A.

(c) Voucher: Botanic Garden, Smith College, Northampton, Massachusetts, U.S.A.

(d) Voucher: Dept. of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona, U.S.A.

NATIONAL BIOLOGICAL SERVICE: INTRODUCTION[1]

P. Mick Richardson[2]

"The establishment of a biological survey by the Department of Agriculture, under a recent act of Congress, should mark the beginning of a new era in the botanical field-work of the United States." One might think that this sentence from an editorial in a botanical journal was written to celebrate the formation of the National Biological Survey in 1993 (National Research Council, 1993). It was actually written one hundred years earlier (Anonymous, 1896). What happened to the proposed biological survey in the intervening century? Perhaps it met resistance of the type that has confronted its belated but necessary successor (Babbitt, 1995; Macilwain, 1995). One day we shall hopefully have a full account of the part of biological history that concerns political opposition to the gathering of basic knowledge and information.

The day before I sat down to write this introduction I noticed a supplement to the journal *BioScience* on the current periodicals shelf in the library at the Missouri Botanical Garden. It was entitled "Science and Biodiversity Policy" and contained a variety of articles about the development of a national strategy on biological diversity, articles that began as papers delivered at the 1994 American Institute of Biological Sciences (AIBS) meeting in Knoxville, Tennessee (Mooney & Gabriel, 1995). I immediately wondered whether we had been scooped and the Missouri Botanical Garden symposium proceedings rendered redundant. However, my fears were unfounded: the two symposia are largely complementary, and, in fact, the *BioScience* publication makes an interesting but rather long introduction to our symposium.

The papers are discussed here in the order in which they were presented on the Saturday of the Systematics Symposium. Ronald Pulliam of the National Biological Service (NBS) began the symposium by outlining the history of the NBS agency in an excellent talk entitled "The National Biological Service: Building a National Partnership." He described how the agency came into being as the National Biological Survey and metamorphosed under political pressure into the National Biological Service. The NBS works with others to provide the scientific understanding necessary to support the sound management and conservation of the nation's biological resources. The paper is not reprinted in these proceedings, but his paper in the *BioScience* volume (Pulliam, 1995) describes the birthing process of NBS. After the coffee break, Meredith Lane (University of Kansas Natural History Museum and National Science Foundation), in a paper entitled "Roles of Natural History Collections," talked about how these collections have related to society at large during a long and evolving history. She urged an abandonment of personal competition in order to complete a compilation of the earth's biota. The morning session was completed by Anne Frondorf, a second speaker from NBS. In the paper "Systematics Information as a Central Component in the National Biological Information Infrastructure," she and coauthor Gary Waggoner describe how NBS is working with various partners to make data more easily available to those who need it when they are making decisions on resource management. The Internet is a powerful tool and essential for the distribution of information that is being generated and/or maintained in a range of biological fields and institutions.

After lunch we were treated to an update in our current understanding of the diversity and relationships of microscopic forms of life. Diana Lipscomb (George Washington University) gave a paper entitled "Biodiversity and Microorganisms," published here as "A Survey of Microbial Diversity." A multikingdom system is necessary not only to accommodate the increasing diversity of microbes revealed by new technologies (my Grammar School biology teacher, Mr. Malkin, frequently informed us that molecular biology and the electron microscope had complicated and thus ruined the study of bi-

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[1] This and the five articles that follow it are the proceedings of the 42nd Annual Systematics Symposium of the Missouri Botanical Garden, *National Biological Survey* (now National Biological Service; see Nevling, 1996, this issue). The symposium was held 6–7 October 1995 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

The symposium was supported in part by the National Science Foundation under grant number DEB-9420140. I thank Nancy Morin for helping to select a fine diversity of speakers, Carol Davit for selfless help in organizing and administrating the symposium, Yevonn Wilson-Ramsey for her fine illustration of three *Papaver* species for the symposium brochure, and the symposium registrants for being such a trouble-free and pleasant group.

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ology), but also to replace the simple four- or five-kingdom systems used in teaching, and in my opinion, misleading, students of biology. This paper is an excellent introduction to recent developments in this field and will be especially useful to those of us who have allowed higher organisms to fully occupy our minds for too many years. The next paper, unfortunately not published here, was given by Rahmona Thompson (East Central University) and was about "The Flora of North America, the National Biological Service, and Electronic Technology." She warned botanists that we must be aware of changing methods of communication and we must also keep up with the revolutionary changes taking place in the publishing process, emphasizing the use of hypertext and the flexibility of digital formats. The final talk of the afternoon reflected the international aspects of the day's program. Nationals of six countries were in the audience of 350 participants. The paper, entitled "An International View of National Biological Surveys," was delivered by Jorge Soberón (CONABIO), and the published form is coauthored by Jorge Llorente and Hesiquio Benítez. The natural history collections in industrialized countries hold large amounts of data in the form of labels on specimens collected in developing countries. The authors advocate a policy of sharing this data in order that the scientists in developing countries will have access to the existing information about their national biota. This is not a completely straightforward task but requires the international negotiation of agreements for the use and ownership of data.

A thought-provoking after-dinner address entitled "The Last Species" was given by Lorin Nevling (Illinois Natural History Survey). It was accompanied by more than a hundred slides. The words and pictures together earned the deliverer a standing ovation. You must read the article for yourself to see what he said, but the gist of it is that he challenged the audience to widen their views of their responsibilities as educators if we would like the world to be still recognizable in the year 3000.

Besides the seven formal papers described above, three other significant events took place during the weekend of the symposium. First, the Mulford Commemorative Luncheon was held on Friday, 6 October 1995, in the Spink Pavilion. A sandwich buffet was followed by two short papers concerning female botanists. The first paper, by Carol Prentice, a botanical historian living in Boise, Idaho, was on the subject "A. Isabel Mulford: Pioneer Botanist" and concerned an interesting woman who taught at Vassar College, gained the first-ever Ph.D. degree awarded by Washington University for her work on *Agave* undertaken at the Missouri Botanical Garden, undertook three expeditions out West in the 1890s, taught high school for a few years, and then seems to have vanished into obscurity until her death. This remarkable history will be forthcoming as further details about Isabel Mulford's life are unearthed. The second paper was more general. It was entitled "Botany: A Place for Women in Science" and was given by Barbara Ertter (University of California-Berkeley), who also plans to publish an expanded version of her talk. The second event took place at lunchtime on Saturday, 7 October 1995. This was the dedication of the Edgar Anderson Memorial Area, a section of the Garden planted with various taxa of *Buxus*. Charles Heiser (Indiana University) spoke about some of the exploits of Dr. Anderson, with whom he had done his Ph.D. work. At the third event, which took place immediately prior to the talk delivered by Lorin Nevling referred to above, an award was presented to John Dwyer in recognition of his services to taxonomy at Saint Louis University and the Missouri Botanical Garden. Altogether, the 42nd Annual Systematics Symposium was an interesting, exciting, and historic meeting.

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ROLES OF NATURAL HISTORY COLLECTIONS[1]

Meredith A. Lane[2]

Abstract

Natural history collections have always contained a wealth of data: genetic and phylogenetic information stored as an inherent part of the samples of organisms themselves, and biogeographic, ecological, and biographical information stored in the labels that are affixed to them. Together, a preserved organism and its label are a scientific specimen that has great intrinsic value. Separately, the label is a piece of paper with meaningless inscriptions upon it, and the plant, spider, microbe, mushroom, or bird, though carefully preserved, is just so much dead organic matter. Natural history collections are the repository of the vouchers for the documentation of what we know about the diversity of living things—what species exist and where, what their habitat requirements are, what ecological associations they have with other species, what useful biochemical products they might generate, and who collected them and has studied them. Before the advent of computers, natural history collections were physical databases from which geographic or ecological analyses and reports could be extracted by human visitation and transcription, usually a laborious and time-consuming task. However, such analyses are invaluable for land-use planning, pharmacognosy, conservation biology, range management, forestry, agriculture, and a host of other applications, including scientific studies of the ecology and systematics of the species being examined. Computerization of label data makes such reports on distribution and ecology of species more readily available to potential users; they add value to the data. Interconnecting the databases brings robustness to the information that natural history collections can provide to policy-making bodies; appreciation of robust data will lead in turn to appreciation of the collections from which those data were taken. Interconnectivity requires that collections personnel abandon competition in favor of achieving a common goal: the discovery and description of the world's biota.

When I was first asked to write this paper, I was told that the topic I would cover should be "the role of natural history collections in relationship to the National Biological Service." I have taken the liberty, while keeping biological surveys in mind, of expanding my topic to include the roles (plural) of natural history collections, not only in relation to the NBS but also in relation to society at large, and to each other.

I begin with a broad-brush statement about the activities of biological surveys in general, and their relationship to collections. Next, I touch on the history of natural history collections—what their roles have been in the past, and how those roles have changed (or not) over the years. Then, I present the perceived roles of natural history collections as they stand and as I think they need to become. Finally, I come full circle to the relationship between natural history collections and biological surveys, and the National Biological Service in particular.

Throughout, when I use the term "natural history collections" I mean collections both of animals and of plants. It is true that botanists have been slow to give up the name "herbarium," a word that de Tournefort and Linnaeus used to mean a collection of preserved specimens of plants. I suspect that we botanists might much more readily have become natural historians of plants had our collections continued to be called, as they were before de Tournefort and Linnaeus (Radford et al., 1974), *hortus siccus* or *hortus mortus*! However, I for one consider herbaria to be natural history collections, and refer to them as such except in the discussion of the history of the two sorts of collections.

Missions of Biological Surveys

IDENTIFY NATURAL (LIVING) RESOURCES

Most biological surveys around this country have as their charge the documentation of the biota of the state or other geographical entity to which they belong. The political entities that established the surveys expect them to provide information to policy-making bodies that will allow for "better decision-making" with regard to those living resources

[1] Craig Freeman assisted with many aspects of this paper, John Simmons pointed me to literature about the history of collections, and Vivian Nolan retrieved it from various libraries, including those of the National Science Foundation and the Smithsonian Institution. I thank both the people and the libraries.

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(as defined in human economic terms). To be able to provide the information requested, biological surveys personnel must extract it from the literature, or perform original research (C. C. Freeman, pers. comm.; Cameron, 1929; Kim & Knutson, 1986; Rautenbach & Herholdt, 1990).

PERFORM TAXONOMIC/ECOLOGICAL STUDIES

It would be desirable, from the political standpoint, for the literature to contain reports of studies that have already been done that would answer the questions of the legislatures. Very frequently, this is not the case, and biological surveys personnel undertake original investigations.

Often, the requests for information involve questions about the ecology of certain organisms. The ecological research, in turn, often involves questions about the taxonomy and phylogeny of those organisms. The answers to these questions rest squarely in natural history collections that the biological surveys personnel may maintain themselves or have access to in natural history museums (Chernoff, 1986; Pettitt, 1994).

If there is no collection, the first step in the research is to make one. Even if the consulted literature does contain a taxonomic, phylogenetic, and ecological analysis of the organisms of interest (so that the biological survey person does not have to do original research), that study would have been based on natural history collections that voucher and document the work of the author(s) of the paper (e.g., Yochelson, 1969; Conference of Directors of Systematics Collections, 1971; Pettitt, 1994).

EXAMINE ENVIRONMENTAL IMPACTS

Biological surveys often examine the environmental impacts of human actions (Kim & Knutson, 1986; Pettitt, 1994) within their own purview or those of neighboring states. Again, it is natural history collections that document the spread of introduced taxa and decline of native species, the current distribution of taxa, and the relationships among organisms, which live, not in clades but rather in interconnected, interoperable habitats. The phylogenetic studies that are done by systematists using the same collections provide the historical context for the evolutionary emergence of the organisms within those habitats.

DEVELOP MONITORING, MANAGEMENT, AND CONSERVATION PROTOCOLS

Within museums lie solutions to problems in conserving natural resources (Shropshire & Shropshire, 1991). The biological surveys are often expected to develop plans to evaluate, monitor, and mitigate all manner of ecological phenomena. Their reports are vouchered and documented by specimens placed in natural history collections; without those vouchers, the facts that their studies have uncovered are in question. These protocols must be developed in light of collections; otherwise there is no basis for the pursuit of one management method over another (Conference of Directors of Systematics Collections, 1971; Rautenbach & Herholdt, 1990; Pettitt, 1994).

Relationship of Biological Surveys to Natural History Collections

From these examples, it is clear that natural history collections are fundamental to all that biological surveys do. Where there is no collection, the first job of a survey is to form one. Such was the situation in 1804–1806, when President Thomas Jefferson, having just acquired the huge Louisiana Territory for the fledgling United States, sent Meriwether Lewis and William Clark and their companions to make a survey of the headwaters of the Missouri River and territories thereabout, to include observations of the minerals, soils, climate, peoples, and animals in their diverse kinds, as well as "... the dates at which particular plants put forth or lose their flowers or leaf, times of appearance of particular birds, reptiles or insects" (Cutright, 1969). Jefferson was himself a naturalist of note, who kept detailed records of the requirements of many sorts of plants that he attempted to grow in his experimental garden, and of observations of the behavior of animals on his plantation (Martin, 1952). Lewis and Clark took their charge from the President seriously, as it was meant, and brought back bales of specimens of various sorts of organisms, sometimes at the risk of life and limb (Cutright, 1969). This leads us to the discussion of the history of natural history collections. I shall in a moment return to Lewis and Clark.

History of Natural History Collections

The geneses of natural history collections are, I have found, in general understood differently by botanists and zoologists. The instigation for collecting plants, and the simple method of their preservation, led to a different beginning for herbaria than for collections of animals, for which specimen-conservation techniques development is still in full swing (Ouellet, 1985; Hawks, 1990).

The origins of natural history collections extend back through Western history to Ptolemy's academy

in third-century B.C.E. Alexandria, which was a palace that contained botanical and zoological gardens for teaching purposes, and cloisters and lecture rooms for students and teachers (Bateman, 1975). Pliny's first-century C.E. *Historia Naturalis* not only describes this academy, but gives our science its name (Porter, 1991). The development of collecting between that time and the Renaissance, unfortunately, is one of war, looting, and plunder, but, by the fifteenth century, palaces in Europe contained collections of books, art (much of which had natural subjects), and the odd natural oddity (narwhal tusks interpreted as unicorn horns, for example) (Ritterbush, 1969; Bateman, 1975).

ZOOLOGICAL COLLECTIONS

Through the sixteenth century and well into the seventeenth, "cabinets of the curious," that contained shells, fossils, minerals, casts from nature, and botanical and zoological art, became a common possession among European nobility (Alexander, 1979; Impey & MacGregor, 1985; Hooper-Greenhill, 1992). Some of these cabinets were actually whole rooms, others were truly pieces of furniture designed to contain objects that represented the entire world in miniature. These objects, however neatly stored, were not scientifically arranged, nor were they available to the public for study—they were private collections amassed for private, primarily aesthetic, purposes (Ritterbush, 1969). Although I do not know this, I would wager that the owners entered into collection-building competitions: "mine is bigger than yours"—the same syndrome that is perpetuated among some museums and collectors today.

The first of the public museums of natural history (which included, from its inception, two herbaria) was that in Paris, founded in 1635; the first university museum was established at Basel in 1671 (Bateman, 1975). The Ashmolean Museum at Oxford University, established in 1683 (Alexander, 1979; Lintz, 1991), seems to be the first to have official curators, a catalog, and a set of regulations for visitors. These early museums, however, were more of art than of actual natural objects, because of the difficulty of preservation of animals. When Charles Wilson Peale, an American, worked out the use of arsenic in taxidermy in the late 1700s, that obstacle was overcome, and natural history collections began to acquire, for the first time, long-lasting collections of birds and mammals (Porter, 1991).

Peale's Philadelphia Museum, started in 1786, does not by many years postdate the establishment of the British Museum of Natural History in 1753 (Lintz, 1991) or the first formal natural history collection in North America, the Charleston Library Society, started in 1773 (Alexander, 1979). Even the venerable Paris Museum only began to acquire birds at the very end of the eighteenth century; by 1793, that collection included 493 skins.

HERBARIA

Modern herbaria, in the post-Renaissance scientific sense, have a history that is at least a century longer than zoological collections. If we accept herbaria as natural history collections (which in this day and age they certainly are), then the oldest formal natural history collection for scientific purposes of any sort (and this, most zoologists do not know) is the oldest herbarium in existence, which dates from 1523 (Ogilvie, 1985). The herbarium of Gherhards Cibo dates from 1532 (Radford et al., 1974), and the herbarium of the University of Padua, begun in 1545, was the first institutional herbarium (Shetler, 1969), and therefore the first university natural history collection. In the New World, the establishment of the first herbarium (at Winston-Salem, North Carolina, in 1772) predates by a year the oldest zoological collection on this continent (Shetler, 1969; Porter, 1991).

The original use of the word "herbarium" is much older even than the sixteenth century. Herbaria once were rooms in medieval monasteries, in which were kept, usually hanging from the rafters, bundles of dried herbs that were to be used for flavoring food, for counteracting mildew and body odors in linens and clothing, and, of course, for medicinal purposes. For an image of such a room, think of the garden and monastery in Franco Zefferelli's lush cinematic production of Shakespeare's *Romeo and Juliet*—in the herbarium, Juliet is presented with the sleeping draft that had been compounded from the herbs hanging overhead. In addition, these examples of dried herbs would have been used in teaching younger monks about the plants and their uses. Thus, the monastery herbarium was both the forerunner of the modern teaching collection of plants, and continuation of the "herbalist" period of botanical history (Radford et al., 1974).

My purpose in painting this sketchy history of natural history collections is three-fold: First, that the term "natural history collections" as a designation of scientific resources should be understood to include herbaria; we should not use the phrase "natural history collections and herbaria" to refer to the collections enterprise, because that distinc-

tion sets us apart rather than bringing us together. Second, that biological surveys have always made and relied upon natural history collections. Third, I stress the connections between herbaria and collections of other sorts of organisms because it is the history of herbaria that is rooted most firmly in the service to society ethic (i.e., the medicinal and agricultural uses of plants). It is this linkage of herbaria, and thereby collections of other sorts of organisms, to societal service that will serve systematics well as it grows into the roles outlined for it in *Systematics Agenda 2000.*

Roles of Natural History Collections in the Past

Originally, natural history collections made it possible for their viewers to have some notion of the biota and artifacts of distant places that they themselves could not visit (Lintz, 1991; Hooper-Greenhill, 1992). Collections were made for entertainment value as "curiosities" (Impey & MacGregor, 1985), and hidden from competitors until their value could be estimated. Plants and shells were collected for their aesthetic value; the early collections of objects were valued originally as the subjects of paintings and drawings, rather than for themselves (Ritterbush, 1969). Collections were made because interest in the natural world was a major preoccupation of Renaissance learning (Impey & MacGregor, 1985), and, according to Albert Bickmore (first director of the American Museum of Natural History), for "teaching our youth to appreciate the wonderful works of the Creator" (Alexander, 1979). The education function evolved later into a view of nature as an open book, from which "the Birds and Beasts will teach thee!" as stated the tickets to Peale's Philadelphia Museum (Lintz, 1991).

Only gradually were repositories for the natural history collections made by survey expeditions such as that of Lewis and Clark identified and established. Despite his intense interest in natural history (Martin, 1952), and his charge to Lewis and Clark to make collections of the organisms they encountered, Jefferson (with, for him, unusual lack of foresight) did not make provision for the storage and curation of the specimens thus acquired. Many of the specimens that Lewis and Clark collected were dispersed (Porter, 1991); only a few were returned to an appropriate U.S. repository. Though the Congress continued to send out many more expeditions that collected specimens during the next several decades, it was not until 1879 that the official U.S. repository for such collections was established: the United States National Natural History Museum (Cowan, 1969; Porter, 1991). Meanwhile, some of the states had initiated natural history collections. Here, New York is a telling example: The New York State Natural History Survey was started in 1836, and that Survey generated a Cabinet of Natural History (that is, collections) as its first task. The cabinet was physically located in Albany in 1843, seven years after the institution of the Survey itself (Porter, 1991). Only after the collections were made were ecological studies instituted. In the nineteenth century it was recognized that collections must be made because they were critical to the progress of science, but provision for the conservation and preservation of the specimens was a harder sell. Today, it is not only the latter but also the former that must be promoted, although natural history collections today occupy prime real estate: for examples, the California Academy of Sciences in Golden Gate Park (San Francisco), the Smithsonian Institution on the National Mall (Washington, D.C.), the Field Museum of Natural History on Lakeshore Drive (Chicago), and the Missouri Botanical Garden on Shaw and Tower Grove Avenues (St. Louis). The taxpayers and contributors that provided this real estate, and the curators who through the decades have built the collections, deserve an appropriate return on their investments (Cowan, 1969; Allmon, 1994; Shetler, 1995).

Present Roles of Natural History Collections

Today, the roles of natural history collections, as is often stated in the literature, are two-fold: research (Lemieux, 1981; Edwards, 1985; Lintz, 1991; Stansfield, 1994), sometimes called the "inner museum function," and education, the "outer museum function" (Humphrey, 1991; Allmon, 1994). Some authors add service to this list as a third role (Laerm & Edwards, 1991; Pettitt, 1994). The things that natural history collections *do*, however, may be summarized in a few statements. Of course, it is possible and reasonable to expand this list into its myriad component parts (as, for example, in *Systematics Agenda 2000*), and there are contexts in which I do, too. However, for the purposes of this paper I will use the "executive summary" form.

Natural history collections record the world's biota in space and time, and document what we do and do not know about that biota (Michener et al., 1970; Conference of Directors of Systematics Collections, 1971; Lamanna, 1976; Dessauer & Hafner, 1984; Duckworth et al., 1993; Anonymous,

1994; Federal Biosystematics Group, 1995). Further, natural history collections are the fundamental and indispensable resource for biological surveys, which study living organisms to understand ecosystem dynamics and conservation of living diversity (Irwin et al., 1973; Edwards & Grotta, 1976; Kim & Knutson, 1986; Duckworth et al., 1993; Anonymous, 1994; Federal Biosystematics Group, 1995). Natural history collections voucher economically important organisms, research in systematics, population biology, ecology, genetics (and a host of other fields), and provide specimens and knowledge for education and exhibits (Michener et al., 1970; Irwin et al., 1973; Lemieux, 1981; Chernoff, 1986; Duckworth et al., 1993; Allmon, 1994; Anonymous, 1994; Federal Biosystematics Group, 1995). Natural history collections are the basis for public and formal education programs (Lemieux, 1981; Allmon, 1994; Anonymous, 1994; Federal Biosystematics Group, 1995). Natural history collections are irreplaceable assets of the greatest value (Brain, 1990).

It is this repository-of-knowledge function, I suspect, that keeps most systematists constantly defending and promoting natural history collections. We understand, and we must constantly be vigilant that others understand, that human beings learn about new things *only in the context of what they already know.* Natural history collections are *the* context for what we already know about the diversity of living things on this planet. Collections are the vouchers for the knowledge to be passed to succeeding generations (Lamanna, 1976). It is estimated that that knowledge is exceedingly skimpy: Perhaps only 1 to 5, or at most, 15 percent of the species on Earth have been apprehended by science. In our research function as the describers of new species, we despair of our ability to discover and describe the remaining 85 to 99 percent (which means tens of millions to a hundred million or more species) in the 40 or so years we have (if we are lucky) before they are mostly destroyed (Anonymous, 1994). But think! How much more difficult would that task be without the comparative research collections we already have of the things that *are* known to science?

Thus, natural history collections personnel have several goals that must be reached. First, we must preserve against the forces of entropy the heritage that is represented by the some two billion specimens (Duckworth et al., 1993) in natural history collections around the world (approximately 400 to 500 million in the U.S. alone). This goal requires constant improvement of our techniques of specimen conservation (Lemieux, 1981; Hawks, 1990), because many if not most of these specimens could not be collected again—too many habitats have been destroyed, and the cost of collecting expeditions has become too high to replicate something someone else has already done. Second, we must continue to collect, to gather new knowledge, and to process that knowledge for the benefit of society and biodiversity itself. Third, and most importantly, we must constantly educate—not just youth, the public, and politicians—but also ourselves.

As natural history collections curators or collections managers or researchers, we must school our competitive instincts into cooperative ones. No longer should the goal be to demonstrate that Kew has more specimens than Paris, the American Museum more than Berlin, my own herbarium in Kansas more than Oklahoma's or Colorado's; in short, to demonstrate that: "mine is bigger than yours." We must teach ourselves better public relations (Grove, 1970; Irwin et al., 1973), political maneuvers (biologists and particularly systematists are especially lax in this area), and yes, even better business practice (Malaro, 1994). We must develop and follow long-range plans and careful acquisitions policies (Hoagland, 1994; Malaro, 1994) that are coordinated among museums to avoid duplication of effort. We are together in a race against time: "Gentlepersons of Collections, rev your engines!" But first, examine your motives. There is no time for the pettiness of competition in this race. Our common goals must be to partition the work of diversity discovery and collection (Anonymous, 1994), conservation and preservation (Hawks, 1990; Herholdt, 1990), and become much better ambassadors both for the work we do, the collections within which we work, and the uncounted millions of species we serve.

Those are lofty, admirable, and incredibly difficult goals. But how do we attempt them, and from whence will the funding come? I believe that we have a start. It is a beginning that needs improvement and modification, not to mention a "pedal to the metal," but a beginning nonetheless.

Twenty to twenty-five years ago, a number of reports and working papers produced by committees of the fledgling Association of Systematics Collections and similar bodies (Manning, 1969; Conference of Directors of Systematics Collections, 1971; Edwards & Grotta, 1976; Humphrey & Clausen, 1977) suggested that computerization for collections management was a direction that natural history collections ought to take. During the intervening two decades, a number of things have happened in this area: (1) quite a number of natural history collections have digitized at least part of their spec-

imen data, (2) the realization of the need for data standards has occasioned the development of some of these within certain collections communities (Biological Collections Data Standards Workshop, 1992), (3) a number of monographers have realized the value of computerizing the data of the specimens they borrow, (4) there have been workshops about natural history collections computerization and networking, and (5) the Research Collections in Systematics and Ecology program of the National Science Foundation has instituted a special category for collections computerization that supports several database-development projects around the country. Most curators and collections managers now recognize the value of digitized collections information, and are willing to expend effort to computerize (Owen, 1990; Allen 1993; Cohn, 1995).

However, progress in this area has been slowed by two factors: (1) the learning-curve difficulties experienced by collections curators and managers in trying to understand fully relational database management systems and Internet connectivity, and (2) the lack of cooperation and agreement within the larger community on database structure, semantics, and syntax—that is, what are collectively called standards, which are important especially as we interconnect our databases. We *must* get past these barriers. As Shetler (1995) has so aptly said, "If our generation doesn't figure out how to provide better access to the information stored in our existing collections, then the next generation may not be able to defend keeping these collections."

Information Management

NOT ONLY FOR COLLECTION MANAGEMENT

Many collections have begun the databasing process with excellent intentions: information provision on a case by case basis to other systematists and natural historians who work within a collections environment. Such databases allow the home collection to develop loan-management software that accommodates the idiosyncratic needs of that particular museum. While such database capabilities are useful within a small sphere, they do little for outreach beyond the systematics collections community.

NOT ONLY FOR THE PURPOSES OF SINGLE STUDIES

Many monographers have databased many specimen records for use in print publications. But once the publication is produced, the data lie dormant in files accessible only by outmoded and outdated programs. There also have been databases produced specifically to answer certain ecological questions. But these databases alone do little to contribute to the store of human knowledge if they are left in storage on a floppy disk in a desk drawer. They contain data plus keystrokes plus analysis—the value-added components—that turn raw data into information. Why should this be withheld from others? Why not share it? In so doing, investigators fulfill both a scientific and a societal obligation.

NATURAL HISTORY COLLECTIONS DATA INFORM AND ILLUMINATE POLICY DECISIONS

Natural history collections have for decades claimed that the data contained in the specimen labels, vouched for by the specimens themselves, are an inestimable information resource for land and resource management, range science, agriculture, pharmaceutical chemistry, DNA sequencing for phylogenetic studies, and myriad other fields. This claim is, in fact, true. However, to put those data to use has for the same duration of years been a time-consuming and tedious task of transcription and collation of the data, requiring that a thorough investigator visit one to several collections or obtain the specimens on loan. Those persons who need these data, but who are not inclined to sit for many hours in quiet among the cases, tend to disbelieve the claim of value of specimens because of the tedium involved in extracting the information. Bad decisions have sometimes been made about the use of biological resources because individuals found it easier to guess or to follow preconceived notions than to obtain real information, even though the needed data were right at hand in the closest natural history collection.

Computerized collections catalogs. In the 1970s, when farsighted curators began to apply computer tools to collections management tasks, the argument for doing so was that natural history collections could more easily track loans, care for specimens, and keep catalogs (e.g., Humphrey & Clausen, 1977). The computerization effort was seen as a boon internal to the systematics community. The accessibility of the data for ecologists and others was regarded as a useful byproduct. Collections were to support systematic research first; managing collections more efficiently by computerizing was to be for the benefit of collections personnel.

Value-added data. Formal curatorial catalogs of natural history collections date at least from the establishment of the Ashmolean Museum; most probably they are older than that, stemming from the jumbled days of the "curiosity cabinets." Originally, catalogs were listings of the kinds of objects

in a collection. With the advent of computerized "catalogs," the meaning has mutated, become much more expansive, and the catalogs, which we now call databases, infinitely more valuable. There are those who fear that the rapid accessibility of information in computerized catalogs will render, in the minds of policymakers and funding bodies, the specimens themselves obsolete. In fact, exactly the opposite is true. The "evolved catalog," because it provides readily accessible information, renders the specimens that voucher it even more valuable. Remember? In the days before computerization, the specimens and their data were often being ignored altogether. Now, the data cannot be ignored, but likewise they are worthless unless vouchered by well-cared for specimens. People who use data want to know that they are real data; those people are therefore more likely, rather than less, to appreciate natural history collections for the inestimably valuable resource that they are.

COLLECTIONS AS CONSERVATION TOOLS

In fact, to humans, *knowing* something almost always makes that something more valuable. Make it possible to *use* the knowledge and the valuation skyrockets. Think, for instance, of oil. Petroleum. Nasty black stuff that bubbled out of the earth; once, it was to be avoided! And now look—humans value "black gold" as much as precious metals, are ready to mortgage entire economies, and even go to war for it, because we can use it because we know its properties. I submit that the same could be true of "biodiversity"—humans must come to know and use biodiversity (and it is to be hoped that that use will be sustainable, unlike the use of petroleum). Then, and only then, it will be *valued* and therefore *saved.* Natural history collections have an important role to play in this scenario. As the caretakers of the human record of biodiversity and what we know about it in the formal sense, presumably we care about the biota of Earth and want to see biodiversity saved.

The task of finding ways to get humans to know, and therefore value, and therefore save biodiversity is one of the great challenges to human ingenuity in our time. Natural history collections contain a vital portion of the information on ways of knowing and utilizing biodiversity. We must have the strength of our convictions that our kind of science has a necessary place among those ways of knowing and utilizing, but we must get beyond our hubristic notion that our science, as we have practiced it in the past, is sufficient to supply all of the needed "ways of knowing and utilizing." We must become entrepreneurial thinkers; we must find ways to add value to our data, and we must make it available and rapidly accessible. By providing high-quality information (value-added data), we will increase the value of our collections, and of biodiversity, in the estimation of our publics.

And so, the question becomes: How do we increase the value of our data and thereby our collections and thereby biodiversity? I believe that finding answers to this question is a role that natural history collections must play now and in the foreseeable future. The data from a single collection, even a large one, cannot by itself answer the big questions. However, those data, interconnected with the data from other collections can together provide a robust answer. We must be continuously conscious of the need to provide outputs of our science that are useful to society. That, recursively, will make our collections and biodiversity more valuable. This means turning our thinking outward.

We must get out from behind our specimen cases—either that, or invite society in, or both. One way or another, we must engage our publics by making it easy for them to know, understand, use, value, and save. I think that this will be easier together than it is for any one institution, or even a group of nine or ten institutions, alone. Natural history collections have in the past five years taken the first, hesitant steps on the road to interconnectivity. It is my purpose here to encourage us all to get in shape and begin the marathon.

INTERCONNECTIVITY

I am borrowing "interconnectivity" from cyberspace and bringing it into the very human level of relationships among natural history collections personnel because the word "community" has been overworked and used to mean something far less grand than I propose. Natural history collections must together become a nationwide museum: a group of interconnected, interrelated, interactive, interdependent nodes on the Internet. As Benjamin Franklin said, "We must all hang together, or we shall surely all hang separately." We must make ourselves indispensable—together we are, individually we are not. We must view ourselves as working not at Missouri Botanical Garden or the University of Kansas or the Smithsonian or Montana State University or the Paleontological Research Institute or the Field Museum or the University of Wyoming or the New York Botanical Garden or Louisiana State University, but rather in the greatest collection of all: the collection of all natural history collections. The good part is that to build

this grand museum we do not need to change physical location, we merely need to get better at cooperating and appreciating each other's strengths. We do not have to become homogenized; in our diversity is our strength. We can easily grow beyond the "mine is bigger than yours" syndrome, because *ours* will be, virtually, enormous.

BENEFITS FOR NATURAL HISTORY COLLECTIONS

In the 1970s, the thought was that computerization would be a good collections management tool (e.g., Conference of Directors of Systematics Collections, 1971; Humphrey & Clausen, 1977), and that analysis of the data by other scientists would be a useful byproduct of the effort. I hope that I have made clear that this notion is actually a better concept if it is turned inside out. We should be computerizing and interconnecting our data for use by other scientists and society. Collections management is a minor, though useful, byproduct of that effort. The benefits of outward-looking and interconnected data sets for natural history collections science itself are many:

(1) The generation of more robust answers to systematic, phylogenetic, and biogeographical questions, because we will have access to ecological data sets as well. Shared, combined information is good information. Good information drives good science; the two are reciprocally illuminative.

(2) "Gap analysis" of our knowledge—what do we know about which taxa? Are data hiding in some small but precious collection somewhere, underused and unappreciated and out of context? Together with information from other collections, seamlessly combined via the Internet, small collections become immediately more valuable, and large ones can fill in interstices without needing more cases, more compactors, more supplies for the adoption of orphaned collections. The large collections, by sharing data and software with the smaller ones, can actually preserve those collections (and the education that is based on them) in place. More education means more knowledge, more appropriate use, more tendency to save.

(3) In turn, knowing what we do and do not know will help us make better acquisitions policy decisions, so that systematics professionals can cover new ground rather than unknowingly repeating our steps.

(4) Interconnectivity will allow each natural history collection to achieve greater outreach than any one could alone. Some collections have no exhibit space—their collections could be featured at one that does. Others may have magnificent exhibit space but might be missing a component needed for a really spectacular display—and that small collection across the country might have the needed contribution. These are win-win situations.

(5) Interconnectivity, because it will allow us to make better decisions, will also reduce our tendency to reinvent the wheel, will reduce competition for scarce resources, and will promote the possibility (because we will be providing robust information that is valuable to society) of finding new resources. Together, we can achieve an efficiency of scale that not even the largest institution can do alone.

All of these benefits of interconnectivity together allow us to move forward with the primary task: discovering, classifying, and understanding the world's biota. Again, efficiencies of scale come into play. Dare I dream that we might one day avoid the production of nomenclatural synonyms and homonyms, and the waste of precious time that such represent, because we can quickly and efficiently look beyond the physical collection and library at hand to see if what we are about to do has been done before?

BENEFITS FOR SOCIETY

The benefits to society of interconnected natural history collections lie in the value-added component. Good information, that is, a more robust data set with value added, drives good policy decisions, allowing for the greatest value to be "mined" from biodiversity in a sustainable fashion. "Good" here includes the concepts of ready accessibility and availability, quality control and assurance, and completeness. It is the last that is more nearly achieved together. We know we will not be able to provide complete information about biodiversity anytime in the near future, if we have thirty to a hundred million more species to discover. But, we do know that there is more information in *all* natural history collections about any one known species than there is in any *one* natural history collection about that species (Conference of Directors of Systematics Collections, 1971). Certainly, the information about all known species in all natural history collections has synergistic, emergent properties that cannot be imagined based on a single collection.

The educational value to society of having all the information from all the natural history collections at the touch of fingertips on a keyboard cannot be estimated. This education, on the Internet, can take many forms: classroom study, individual exploration, discussions with curators via CU-See Me or

even more cutting-edge technologies, or informal education opportunities set up and designed to be Web-accessible, to name but a few. Together, we have the wherewithal to put in motion the excellent ideas of individuals who alone may be unable to realize them.

I would like to make one final point here that brings our future role full circle to one of the past roles of collections: entertainment. The "cabinets of curiosities" were for the entertainment and personal satisfaction of their owners. People like to be entertained. They like to feel that they have ownership in something larger than themselves. If they are entertained, they will support and contribute. If there is any doubt of this, just take a look at professional athletic teams. The Internet offers us the opportunity to make natural history collections *entertaining*. Let us not lose the chance to gain new contributors because we are too focused on formal educational tools, formal scientific endeavor, and the esoterica of which only systematists are capable. An easy leap, once we grow past our tendency to compete among ourselves, is to let our enormous "curiosity cabinet" be their enormous "curiosity cabinet"—and I believe that people will feel that they have ownership in something larger than themselves, and will contribute to it. Certainly a nationwide virtual museum will be an entity larger than any of us, but we will all have ownership in it. Go collections! Go connections!

Natural Partners

Biological surveys in general are, of course, the most natural of partners of natural history collections in this enterprise. There are many users of collections data, and these also will be served by natural history collections interconnectivity. But, it is the work of biological surveys, with their connections to natural resource users, that are most understandable to our common general public and the decision-making bodies that rely on them. In turn, biological surveys cannot provide good information to drive good decisions without natural history collections (LaRoe, 1995). Biological surveys and natural history collections are already inextricably interconnected. Both sides of the partnership benefit from ready accessibility of information and appreciation, one by the other, of the role that each plays in the societal arena.

The National Biological Service of the United States has a slightly different character than the state-level biological surveys about which I have been speaking, in that it sees itself as an organizer of existing information, and a catalyst for needed work throughout the nation. It plans to be a clearinghouse, a networking node that will put potential collaborators in touch with each other and with needed information. Again, interconnectivity. Natural history collections have everything to lose if we do not engage in the several partnerships that will be thus formed, and everything to gain if we do become a strong, interconnected web that studies and conserves an increasingly fragile web of life.

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SYSTEMATICS INFORMATION AS A CENTRAL COMPONENT IN THE NATIONAL BIOLOGICAL INFORMATION INFRASTRUCTURE

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ABSTRACT

The National Biological Service (NBS) is leading the development of the National Biological Information Infrastructure (NBII), a distributed network of biological data and information available electronically over the Internet. The important role of systematics information in the NBII is discussed by presenting a vision of a "national systematics information infrastructure." Several current initiatives of the NBS that directly contribute to developing such a systematics information infrastructure are described.

The mission of the National Biological Service (NBS) is to work with other agencies and organizations to provide the scientific understanding and technologies needed to manage the Nation's (i.e., the United States') biological resources. A fundamental part of this mission is to make data and information on biological resources more accessible for more people to use in making resource management decisions. (For the purposes of this discussion, the term "data" refers to material as originally collected or developed, while "information" refers more broadly to material that has been processed, or integrated with other material, or displayed or presented in certain ways. The objective of the NBS and the National Biological Information Infrastructure is to make *both* data and information more broadly accessible.) A key element of the NBS program is development of a national partnership for sharing biological information: the National Biological Information Infrastructure (NBII). The NBII concept is a significant component of the recommendations made by the National Research Council in its 1993 report entitled "A Biological Survey for the Nation."

The goal of the NBII is to establish a distributed "federation" of biological data and information sources, relying on a network of partners and cooperators to make the data they generate and/or maintain available to others throughout this federation, using the Internet. The basic NBII philosophy is to encourage and facilitate biological data stewardship. Under this philosophy, the management of databases remains with those who are responsible for the data, using the "information superhighway" to interconnect and disseminate these data to others.

In addition to biological data and information, new types of software tools providing new capabilities will also be available over the NBII network, to help users work at their own local computer with the actual data from several different remote sources, or to work collaboratively with others at remote sites by using the network (i.e., virtual laboratories). The NBII will also point to sources of biological science expertise: people and organizations that users can contact to get assistance in finding and understanding biological data.

The NBII is being implemented in three sequential phases. The NBII Directory is currently pointing users to biological databases and information sources, within NBS and from other agencies or organizations. The NBII Clearinghouse is also now in operation, with several sites serving metadata describing and documenting their data holdings and, in some cases, also the data themselves. (The term "metadata" refers to data which serve to describe other data, including such things as how, when, where, and by whom the data were collected; the subject matter of the data; indications of data quality; and information on how to obtain or access the data. In a library, for example, if the books are considered "data," the information in the card catalog would be the "metadata.") The NBII Distributed System is the ultimate goal of the NBII and is expected to be operational by 1998. In this phase, users will be able to directly access, retrieve, com-

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bine, and analyze biological data from different sources at different locations (i.e., a virtual national biological database).

Current Emphases in NBII Development

NBS is working simultaneously on three fronts in implementing NBII: (1) making the most significant biological data and information products from NBS research and inventory programs electronically accessible; (2) supporting the efforts of many public and private partners to make their significant biological data and information accessible to others over the NBII; and (3) working cooperatively with other agencies and organizations on the tools and standards needed to provide the infrastructure components of NBII.

Examples of significant biological data and information currently available from NBS through NBII include the North American Breeding Bird Survey, data from the nationwide GAP analysis program, wildlife health bulletins, and data on nonindigenous aquatic species, including the zebra mussel. We continue to work with the NBS science centers, cooperative research units, and other offices to identify NBS biological data and information holdings, and to systematically proceed with cataloging, describing, and electronically serving the most significant of these on NBII.

Partner agencies and organizations, including federal and state agencies, private groups, universities, museums, herbaria, and libraries, have by far the bulk of the biological data and information in the country. Thus, we are working with many partners to make the biological data and information they have more accessible over NBII. Key areas of interest for NBS in developing these partnerships are with other federal agencies, with state resource agencies, and with the systematics and collections management community.

Many of these partners already are making data and information accessible over the Internet, and NBII is linking to these providers, such as the National Wetlands Inventory database of the U.S. Fish and Wildlife Service, the Global Change Master Directory of data and information, and metadata and data in the National Spatial Data Infrastructure. Other agencies and organizations are interested in working with NBS to help automate, describe, and serve their information, some of which may not currently be available in electronic format.

NBS is also working with partners on developing, adapting, and refining the types of software tools, protocols, and standards that are needed to allow users to access, compare, exchange, and use a variety of different data and information sets throughout a widely distributed electronic federation of sources.

NBS has taken a leadership role in developing a draft metadata content standard for use in documenting biological resource data and information in NBII. A metadata content standard specifies what metadata items (fields) to use in describing a data set and how these fields should be formatted and presented. Standardizing the format and presentation of metadata in this way makes it easier for people to compare and contrast among different distributed data sources. The draft standard provides an overall framework for all biological metadata, linking with the Federal Geographic Data Committee standard for spatial data, as well as with the U.S. machine readable cataloging (USMARC) standard for library materials/publications. NBS has contracted with the American Institute for Biological Sciences (AIBS), which assembled a distinguished panel of biological scientists that has provided peer review and recommendations on this draft standard. The final AIBS report has been completed, and NBS will be testing and evaluating this standard and will provide it to other partners who might also be willing to test the standard and provide comments for NBS to use in further revision.

We are also developing and testing new types of software tools and approaches for serving and accessing biological data and information over the Internet. This includes tools for distributed searches, distributed computing, and development of new controlled vocabulary systems to use in searches.

Importance of Systematics Data and Information in NBII

Systematics data and information are of fundamental importance in building the NBII. Systematics data and information are necessary to support biological inventory, monitoring, and research. Systematics collections data can be applied in long-term biological or ecological research or to analyze long-term environmental trends. Use of standardized taxonomic nomenclature supports data sharing and comparison between agencies and organizations. Museum collections also provide essential outreach and education services to raise public awareness and understanding of biodiversity.

Systematics data are collected and maintained throughout a widely distributed network of collections, museums, herbaria, botanical gardens, universities, natural history surveys, and other public and private agencies and organizations. In many cases, availability of different systematics data and

information may not be fully known by the people who would be able to use it. Also, much useful data, such as the information on biological specimens housed in museums, are not currently available in an automated format and therefore are not easily accessible. In addition, integration of information from two or more different sources to help answer questions does not always occur because the data from different sources cannot be easily compared or combined.

It is clear that systematics represents a microcosm of all of the issues involved in implementing the NBII. Building on the overall NBII effort, our goal is to help develop and support a "national systematics information infrastructure" in which data, information, and tools are electronically accessible in a distributed network for a broad array of different applications by a variety of users.

Objectives in Developing a National Systematics Information Infrastructure

1. Support the development and use of data and metadata standards, protocols, and tools or technologies to increase the ability to access, understand, share, compare, exchange, and use systematics data and information from many different data and information providers.

2. Support the development of comprehensive surveys and resource directories of the sources, status, and extent of systematics expertise, data, and information.

3. Develop and implement a program that combines small, targeted tactical investments in certain areas where there are opportunities for pilot or demonstration projects, with larger, more strategic investments on major fronts.

4. Actively pursue and develop partnerships in all areas to help meet mutual needs.

Current NBII Initiatives in the Systematics Information Arena

INFRASTRUCTURE DEVELOPMENT

NBS has several activities under way to support development of the tools and standards needed to support a nationally (and internationally) distributed systematics information infrastructure. NBS is an active participant (along with several other federal and state agencies, private organizations, and international organizations) in the development of the Interagency Taxonomic Information System (ITIS). ITIS is the first comprehensive national database to provide quality information on the scientific nomenclature and taxonomy of all U.S. flora and fauna. ITIS can be accessed on the World Wide Web at http://www.itis.usda.gov/itis.

As described above, NBS has developed a proposed metadata content standard for use in documenting non-geospatial biological data and information on NBII. As this proposed standard is refined, tested, and released over the next year, NBS is working to ensure that it includes appropriate elements on systematics/taxonomy and that the proposed standard is beta tested on actual selected systematics data sets to review its utility and applicability. NBS will also work to disseminate information on applicability and use of a metadata standard to the systematics community.

NBS is also working with numerous partners on several fronts to develop a Standardized National Vegetation Classification System. The major effort is in conjunction with two NBS vegetation mapping programs, the National Park Vegetation Mapping program and the National GAP Analysis Program. NBS is working closely with The Nature Conservancy and the network of State Heritage Programs in the development of this draft classification. NBS is also actively working with other federal agencies on the Vegetation Subcommittee of the Federal Geographic Data Committee to develop and adopt national standards for vegetation classification and analysis. Development of these standards will support the coordinated production of uniform statistics on and mapping of the nation's vegetation among all the federal agencies and other cooperators. By sharing in a common reference system for how vegetation cover is classified and described, agencies and organizations that collect and analyze data about vegetation and distribution, trends, etc., can more easily share and exchange their data. And finally, NBS serves on a special panel of the Ecological Society of America charged with assisting in the evaluation and development of a standardized national vegetation classification system.

NBS is also working to foster development, enhancement, and transfer of tools, technologies, and approaches to support the national (and international) systematics information infrastructure. Key areas where tools and approaches are needed include: (1) cost-efficient approaches to large-scale automation of specimen data that are not currently automated; (2) georeferencing of specimen data that are not currently georeferenced; and (3) visualization and imaging tools to allow for electronic "viewing" of specimens.

One example of the work that NBS is supporting in this area is a project to convert vertebrate distribution records of the original Biological Survey in the Smithsonian's National Museum of Natural

History to digital format, with digital geographic coordinate data from a digital gazetteer that links geographic place names to geographic coordinates. The locality database will be available electronically through NBII. Next, records from this biological survey locality system will be matched to localities associated with specimen records in the National Museum's vertebrate specimen databases. This will add geographic coordinates to all matched vertebrate specimen records in the National Museum's database.

Under the NBS State Partnership Program, a competitive program through which NBS supports state-level biodiversity research, inventory, and information transfer activities, NBS is supporting work at the Florida Museum of Natural History to catalog uncataloged ichthyological materials, automate specimen data, and make the ichthyological specimen data accessible electronically over NBII.

INFORMATION RESOURCE DIRECTORIES

NBS is currently supporting development of four comprehensive information resource directories that are pertinent to the systematics community. NBS and the Association of Systematics Collections are cooperating in the development of two major directories of taxonomic resource information for North America. One is a directory of taxonomic experts and their respective areas of expertise, the other is a directory of research systematics collections, including information on the electronic accessibility of each collection's specimen data. Both of these directories will be served on NBII and will include direct links to any data or information products that are already available on the Internet.

NBS and The Nature Conservancy (TNC) are cooperating on development of a Natural Heritage Network "node" on the NBII, which will include information on each of the 50 state natural heritage programs in the United States, plus national-level data summaries and information products from TNC, available on-line. NBS and the Fish and Wildlife Information Exchange are cooperating on development of a directory of state-level biodiversity databases, which will also be accessible over NBII.

Each of these directories will obviously provide an accessible source of information on systematics resources (e.g., systematics expertise, systematics collections, state-level biodiversity databases) for people to use. More importantly, each will also provide a baseline view of the current situation in these areas (i.e., what information resources are available to what extent in what areas) and lead to the identification of additional measures needed to achieve the overall goal of a distributed systematics information infrastructure. For example, they can highlight major taxonomic groups for which significant systematics data are not yet electronically accessible, or new types of tools or protocols needed to support a distributed systematics data network. This information will be used to guide future NBII priorities in the systematics arena. Under a Memorandum of Understanding with the National Science Foundation, NBS hopes to pursue joint efforts to support new projects that focus on these priority areas.

DEVELOPING PARTNERSHIPS

As noted above, effective partnerships are key to successful development of the NBII and its systematics component. Partner agencies and organizations maintain most of the significant systematics data; partnerships are needed to jointly develop new software tools and new data and metadata standards; and partnerships are needed to provide the funding resources to support more strategic investments in this area.

One recent example of an exciting partnership in this area is a proposed pilot project among NBS, the Smithsonian's National Museum of Natural History, and the Mexican Commission for the Understanding and Use of Biodiversity (CONABIO). The objectives are to demonstrate and test the feasibility of automating and georeferencing data on selected specimens in the Smithsonian collections that were collected in Mexico, as the basis of developing a distributed "international electronic catalog of Mexican specimens." This project will be done as a pilot to test the methodology and approach and evaluate costs and benefits to the participating agencies. If successful and cost-effective, the approach could be used on other portions of Smithsonian natural history collections and/or in other institutions with Mexican specimens.

CONCLUSIONS

The White House Interagency Subcommittee on Biodiversity and Ecosystem Dynamics has identified systematics as a research priority that is fundamental to ecosystem management and biodiversity conservation. This primary need identified by the Subcommittee requires improvements in the organization of, and access to, standardized systematics information on nomenclature, classification, and collections. Working with many partners, NBS is striving to make the valuable data and information embodied in the systematics community, in-

cluding the Nation's natural history collections, more accessible to land use decision makers, resource managers, researchers, students, and the public in general. Through championing the National Biological Information Infrastructure concept, NBS is providing leadership to those collecting and using biological data and information in the pursuit of informed decision making about the wise use and conservation of the Nation's biological heritage.

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A SURVEY OF MICROBIAL DIVERSITY[1]

Diana Lipscomb[2]

Abstract

The development of new technologies is increasing our understanding of prokaryotic and eukaryotic microbial diversity in terms of abundance, diversity, and ecological function. New studies reveal greater diversity than was previously known and have highlighted the importance of these organisms in ecosystem function. There is no consensus on the phylogenetic relationships of the various unicellular organisms at the phylum and kingdom level, and, as long as new taxa and characters are discovered, innovations in classifications of the kingdoms will likely continue. Some general conclusions are already clear. First, it is obvious that classifications that divide organisms into just two, three, four, or five kingdoms are too simplistic. In all of these simple schemes, one or more of the kingdoms ultimately contains a heterogeneous group of diverse taxa and is either paraphyletic or polyphyletic. Alternatively, a multi-kingdom system provides a more realistic view of the diversity of life. Concomitant with this is the realization that some traditional categories such as monera, algae, protozoa, or fungi can no longer be considered distinct phylogenetic groups. An overall scheme of classification that reflects our growing databases will hardly look like those followed in many textbooks, but it will reflect more accurately the relationships of the unicellular microorganisms.

Today, most people are aware of the economic and ecological importance of multicellular animals, plants, and fungi. But this appreciation does not usually extend to the importance of biological diversity of microorganisms. Possibly this is due to the scale at which most microorganisms live. The majority are too small to observe with the naked eye. Many are able to move and constantly change position and so cannot be easily tracked. They have short lives ranging from a few hours to a few days, but they can also form protective cysts and remain in the environment in an inactive state for years. Microorganisms can respond rapidly to changing conditions in their environment, becoming active and growing, or inactive and encysted within minutes or a few hours. All of this makes them more difficult for scientists to study and for many people to relate to and understand. Nevertheless, awareness of microbial diversity is important both because humans depend on microbes for many ecological services (production of oxygen, mineral and nutrient cycling, etc.) and because some forms are agents of disease. It is the purpose of this paper to try to convey something about the diversity of the microbial world: what is known and what is uncertain, and the prospects and challenges for surveying microbial diversity.

Scope of Microbial Diversity

Microorganisms include both prokaryotes and unicellular eukaryotes (the protists). They are ubiquitous and in great abundance in all natural water, sediment, or soil, and are in symbiotic association with multicellular organisms. Information about the size and nature of microbial populations is very incomplete because of difficulties in detecting and extracting them from the environment. Nevertheless, by piecing together various sources of information (and taking into account that activity and biomass measurements can be artifacts of the methods used) we are beginning to understand microbial diversity in terms of abundance, diversity, genetic variability, and ecological function.

ABUNDANCE

Microbial populations may show marked differences over very small distances (McAlice, 1970; Krumbein, 1971; Ashby & Rhodes-Roberts, 1976) or change in intervals as short as a few minutes during environmental flux (Erkenbrecher & Stevenson, 1975). Even taking this into account, in many environments numbers of microbial cells are high. For example, Fenchel (1992) recently estimated that a one-centimeter core of coastal marine sediment contained 4×10^{10} bacterial cells, 10^4 heterotrophic flagellates and amoebae, 10^8 chlorophyll *a*-containing microorganisms, and 2000 ciliates.

DIVERSITY

Microbial communities can also be made up of many different species. Many eukaryotic microorganisms can be identified by a taxonomic expert using standard microscopical methods (e.g., Fois-

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sner, 1991). Using silver stains and light microscopy, for example, Finlay et al. (1993) studied the kinds of ciliated protists (phylum Ciliophora) inhabiting the sandy sediment of a Spanish stream. They sampled this stream on just one day in winter (water temperature was 4°C at the warmest time of day). They marked out 1 square meter, and took from it 13 random sediment samples by pushing a 3-cm-diameter tube 3 cm into the sand, capping it, and extracting the sand. From this small amount of sand, they identified 65 species of ciliates belonging to 50 genera, from 17 orders. Considering the broad diversity of ciliate habitats available within the area, the importance of physical transport processes in the river basin, and the fact that many ciliate species have a cosmopolitan distribution, it is probable that the species richness they recorded is representative of the sandy sediment of the river in winter.

Analysis of the diversity of prokaryotic microorganisms is more difficult because they often lack enough morphological complexity to be accurately identified using microscopic methods. Traditionally, culturing techniques were used to recover prokaryotes from the environment and to characterize them by their physiological and nutritional requirements. Because none of these culturing methods permit the isolation and characterization of all prokaryote species, microbiologists attempted to obtain meaningful diversity data from the use of a wide range of techniques, each of which permits the study of a small fraction of the total marine biomass (Austin, 1988; Button et al., 1993). Even so, only a small percentage of the prokaryotes that actually exist in a habitat are revealed by these methods (Brock, 1987; Staley & Konopka, 1985).

More recently, modern molecular genetic techniques have enabled microbiologists to detect more microbial taxa (Stahl et al., 1989; Bull et al., 1992; Embley & Stackebrandt, 1994; Amann et al., 1995). These molecular tools allow microbiologists to extract and analyze nucleic acid sequences (primarily rRNA sequences) directly from the environment, thus circumventing the need to culture prokaryotes before identifying them. The first studies characterizing prokaryotes directly from environmental samples used sequences of electrophoretically separated 5S rRNA molecules (Stahl et al., 1984; Lane et al., 1985; Stahl et al., 1985). These techniques were refined for 16S rRNA (Olsen et al., 1986) and made easier to perform with the advent of polymerase chain reaction (PCR) technology. This modified approach was used by, for example, Giovannoni et al. (1990) to characterize the diversity of bacterioplankton in the Sargasso Sea and revealed evidence for a previously unrecognized photosynthetic bacterium and a unique heterotrophic bacterial group.

An alternative molecular approach involves cloning cDNA transcribed from 16S rRNA using a primer complementary to the universally conserved region of rRNA (Ward et al., 1992; Weller & Ward, 1989). Ward et al. (1990) used this method to study the thermophilic (~50°C) microbial community from Octopus Spring in Yellowstone National Park. Although this community had been previously studied by more traditional methods and was believed to be relatively simple (Ward et al., 1987), the analysis of the cDNA revealed eight distinctive bacterial groups that did not match sequences known for cultured species including those previously isolated from hot springs.

Since these first studies, such molecular methods have facilitated our exploration of the free-living diversity of marine and estuarine waters (e.g., Schmidt et al., 1991; DeLong, 1992), organisms colonizing solid surfaces (Amann et al., 1992), organisms in water treatment activated sludge (Wagner et al., 1993), and organisms in soil (Torsvik et al., 1990; Masters et al., 1991; Stackebrandt et al., 1993). These methods have also been used to describe microorganisms living in association with other organisms, such as the chemoautotrophic bacteria symbiotic in invertebrates living near hydrothermal vents (Stahl et al., 1984; Distel et al., 1988), the cellulolytic nitrogen-fixing symbiotic bacteria that enable shipworms (wood-boring molluscs) to use wood as a principal source of food (Distel et al., 1991), the prokaryotic symbionts of various protists (Embley et al., 1992; Springer et al., 1992; Embley et al., 1993), the bioluminescent bacterial symbionts of fish (Haygood & Distel, 1993), and the cellulolytic symbionts in the rumen of mammalian herbivores (Angert et al., 1993), and to identify both plant and animal pathogens (e.g., Relman et al., 1990; Gundersen et al., 1994).

Caution must be used in interpreting results because the new molecular methods can be problematic. In addition to technical problems, such as probe sensitivity in certain conditions, it can be difficult to retrieve sequences of rare organisms (Amann et al., 1995). Furthermore, PCR probing of mixed DNA samples can suggest the presence of nonexisting organisms by forming chimeric sequences assembled from sequences of different species (Liesack et al., 1991). Nevertheless, it is obvious that molecular techniques provide extremely useful tools for analysis of microbial diversity (Stahl & Kane, 1992).

ECOLOGICAL FUNCTION

Microorganisms fill diverse ecological roles, and practically all key environmental processes are driven by microbial diversity. Microorganisms are essential to biological nutrient cycling, sulfur oxidation and reduction, ammonification, methanogenesis, and methane oxidation. Symbiosis with microorganisms is a major route by which many multicellular eukaryotes have gained access to complex metabolic activities (Douglas, 1994). These include nitrogen fixation, production of essential amino acids and vitamins, cellulose degradation, and photosynthesis. Microorganisms are essential to all major food webs. A breakdown of the annual carbon fixation and oxygen production by an individual photosynthetic microbe group is not available. It has been estimated that up to as much as 80% of the production of the open ocean is contributed by photosynthetic protists (Platt et al., 1983; Takahashi & Beinfang, 1983; Andersen, 1992), and in lakes chrysophytes (protists) and cyanobacteria contribute up to 40% of the primary productivity (Konopka, 1983).

In ecosystems that lack direct photosynthetic input, microorganisms are even more important as primary producers. Chemoautotrophic bacteria in environments such as deep sea vents and marine sediments provide energy to support a rich assemblage of heterotrophic microbes and animals (Jannasch & Taylor, 1984; Cavanaugh, 1994).

Despite the enormous production of autotrophic microbes, continual grazing by heterotrophs keeps their numbers in check. Some of the biomass produced by photo- and chemo-autotrophic microorganisms is consumed directly by animals (e.g., the echinoderm *Holothuria atra* obtains 10–40% of its carbon from bacteria; Moriarty et al., 1985), but the majority is consumed by heterotrophic microorganisms either from pools of dissolved organics, or as decomposers and primary consumers (Pomeroy, 1974; Williams, 1981; Fenchel, 1982, 1986, 1987; Azam et al., 1983; Ducklow, 1983; Hagström, 1984). These heterotrophs include prokaryotes, protists, and their protistan predators (Azam et al., 1983, Pomeroy, 1984; Williams, 1984; Sherr & Sherr, 1988). Ciliated protists (phylum Ciliophora) are especially important trophic links in these microbial food webs in that they are major consumers of planktonic bacteria, pico- and nano-planktonic autotrophs, diatoms, dinoflagellates, other ciliates, and heterotrophic flagellates and amoebae, and they are eaten in turn by animals such as zooplankton and planktivorous larval fish (reviewed in Pierce & Turner, 1992).

SYSTEMATIC DIVERSITY

As more is being learned about microbial diversity, it is becoming clear that commonly used classification schemes (e.g., Jahn & Jahn, 1949; Whittaker, 1969, 1977; Margulis & Schwartz, 1988) are oversimplified and simply inadequate for describing the true nature of the diversity, and that multiple kingdoms are needed (Leedale, 1974; Taylor, 1978; Lipscomb, 1985, 1989, 1991; Woese et al., 1990). Certainly the changes and rapid proliferation of new classification schemes of microorganisms are confusing to many, but they represent an invigorating period in microbial research from which a new, and hopefully more realistic and stable, system of microbial classification will emerge.

PROKARYOTE SYSTEMATIC DIVERSITY

In contrast to plants, animals, and even eukaryotic microorganisms, the morphology of prokaryotic microorganisms is, in general, too simple to serve as a basis for classification (Olsen & Woese, 1993; Amann et al., 1995). Classification traditionally depended on isolation by culturing followed by characterizing organisms according to physiological and biochemical traits. However, much of our understanding of prokaryote phylogeny is quite recent, due largely to the recent advent of modern molecular genetic sequencing methods. Sequences from ribosomal RNA, for example, have revealed two distinct groups of prokaryotes. This distinctiveness caused Woese et al. (1990) to propose a new superkingdom category, the domain, and to create three domains: Archaea (for the archebacteria), Bacteria, and Eucarya (for the eukaryotes). Despite criticism of this system (e.g., Cavalier-Smith, 1993), it is in widespread use today.

Archaea and Bacteria are both prokaryotic, but the archebacteria have no peptidoglycan in their cell wall, have membrane lipids composed of branched carbon chains attached to glycerol by ester linkage, use methione as the start signal for protein synthesis, lack the rRNA loop that binds ribosomal protein in the eubacteria, and lack the common arm sequence (guanine-thymine-pseudouridine-cystine-guanine) of the tRNA found in all eukaryotes and eubacteria.

Least squares analysis of ribosomal RNA indicates two major groups of Archaea (Embley et al., 1994). One branch, the Crenarchaeota, includes a homogeneous group of sulfur-dependent extreme thermophiles. The other group, the Euryarchaeota, is more heterogeneous and includes methanogens (anaerobes with the ability to get energy by anaerobically biodegrading substances to methane—an

economically important biotechnology used worldwide both to reduce waste and generate fuel-grade biogas [Reeve, 1992]), extreme halophiles (Archaea living in high salt environments), and miscellaneous thermophiles (Woese, 1987). This classification is controversial and has inspired a limited debate over the best way to analyze DNA sequence data, as well as the appropriateness of relying on a single molecular sequence (in this case the ribosomal RNA) (see, for example, Lake, 1987, 1989; Rivera & Lake, 1992). Hopefully, as more data from different molecules are accumulated and systematists of prokaryotes become more sophisticated about phylogenetic analysis, a better substantiated hypothesis of archebacterial relationships will emerge.

The true Bacteria, or Eubacteria, have a peptidoglycan cell wall, membrane lipids composed of straight carbon chains attached to glycerol by ester linkages, an rRNA loop and the common arm sequence of the tRNA, and they use formylmethionine as a start signal for protein synthesis. Neighbor joining analysis indicates that there are approximately 13 groups of eubacteria (Embley et al., 1994), but because not all have been surveyed, those needing further investigation are temporarily placed in descriptive categories rather than formal taxa:

1. *Aquifex-Hydrogenbacter*—organisms that oxidize H_2 or reduce sulfur compounds at extreme temperatures (up to 95°C). Some authors have suggested that these may be phylogenetically intermediate between the remaining bacteria and the Archaea.
2. *Thermotogales*—two genera from geothermally heated marine sediments.
3. *Green nonsulfur or filamentous bacteria*—although most (e.g., *Chloroflexus*) are photosynthetic, a few of these thermophilic bacteria are nonphototrophic.
4. *Planctomycetales*—this group contains budding organisms that are often found attached to surfaces by holdfasts. These organisms have some unusual features for bacteria; at least one species has a membrane-bound nucleoid (Fuerst & Webb, 1991), and their rRNA operon is different from other bacteria in that the 16S and 23S genes are separate (Liesack & Stackebrandt, 1989; Liesack et al., 1992).
5. *Deinoccaceae/Thermus*—this group includes just two genera: the radiation resistant *Deinococcus* and the chemoorganotrophic thermophile *Thermus*, both of which have atypical cell walls containing ornithine in place of diaminopimelic acid in its peptidoglycan.
6. *Spirochaetes*—this group, which was originally recognized on the basis of its unique morphology and mode of motility, has been confirmed by analysis of rRNA.
7. *Chlamydia*—this group consists thus far of only one genus, *Chlamydia*, whose members are all intracellular parasites responsible for a number of sexually transmitted diseases and trachoma (a form of blindness).
8. *Actinomycetales*—gram-positive bacteria which may form branching chains that superficially resemble the filamentous bodies of fungi. They are notorious for species that cause tuberculosis and leprosy, but most are free-living soil microbes of interest to pharmaceutical companies for their ability to produce antibiotics that retard the growth of other bacteria.
9. *Proteobacteria*—this large, diverse group includes the purple sulfur bacteria and their relatives. Many of the organisms in this group are phototrophic and use the pigment bacteriochlorophyll, which absorbs longer wavelengths than other chlorophylls. It has been hypothesized (but not yet rigorously tested using phylogenetic methods) that the ancestor of this group was photosynthetic and that physiological diversity characteristic of the group arose as a result of the exchange of photosynthetic capacity for other physiological processes (such as sulfate reduction) as the bacteria expanded into new ecological niches. The group thus contains a diversity of bacteria including, in addition to the purple bacteria, sulfate- and sulfur-reducing bacteria, fruiting myxobacteria, enteric bacteria, free-living and symbiotic N_2-fixers, and sulfide-oxidizing taxa.
10. *Bacteroides-Flavobacterium*—this group consists of several genera forming a major clade of gram-negative bacteria. It includes a mixture of physiological types including obligate anaerobes (e.g., *Bacteroides*) and obligate aerobes (*Sporocytophaga*).
11. *Gram-positive bacteria with low G+C%*—included here are the endospore formers, lactic acid bacteria, most cocci, the coryniform bacteria, and mycoplasms.
12. *Cyanobacteria*—the blue-green algae, like eukaryotic plants, use chlorophyll *a* and two photosystems in tandem to transfer electrons from water to $NADP^+$ releasing O_2 as a waste product.
13. *Green sulfur bacteria*—these bacteria are photosynthetic but use only one photosystem to

transfer electrons from H_2S (rather than water) to $NADP^+$.

That these groups are natural phylogenetic lineages of Archaea and Bacteria still needs to be tested with cladistic analysis. Furthermore, the ability of the rRNA molecule to give significant support for the deep branches of these trees needs to be investigated.

Eukaryote Diversity

Unicellular eukaryotic microorganisms are usually collectively referred to as protists. For many years, protistologists complained that an understanding of the phylogenetic relationships of the unicellular eukaryotes was hampered by the paucity of their fossil record and their microscopic size (see Corliss, 1974). These barriers are coming down, resulting in great research activity from which a new picture of protist relationships is emerging. The reasons for recent advances are twofold and obvious: First, with the widespread use of transmission electron microscopy, confocal microscopy, and molecular genetic sequencing, microscopic size is no longer a hindrance to gathering character data on these organisms. In fact, unicellular eukaryotic microorganisms possess a level of cellular and molecular diversity that far exceeds that found in multicellular eukaryotes, and this diversity provides a wealth of information for reconstructing their phylogeny. Second, systematists have refined their empirical methods—largely thanks to the cladistic revolution—and it is possible to sort through and analyze the new characters in meaningful ways.

One of the major changes that has emerged from these studies is the realization that the group is *not* a cohesive, taxonomic group that stands as an ancestral hub from which the other eukaryotic kingdoms are derived. Instead, the protista is paraphyletic, not monophyletic, and contains a heterogeneous mix of organisms at intermediate levels of organization and equivocal boundaries with multicellular taxa. A paraphyletic taxon is united by the possession of shared primitive characteristics (symplesiomorphies) rather than uniquely derived characteristics, and its members thus do not have ancestors unique to just themselves and lack unique individual histories (Hennig, 1966).

When unicellular forms are determined to be an organizational grade along lineages leading to multicellular taxa, the unicellular forms should be included in the group with their multicellular relatives. For example, there is no kingdom-level boundary between the unicellular chlorophytes and the green plants, the choanoflagellates and the sponges, or the chrysophytes and the multicellular brown algae (Lipscomb, 1989). Not all unicellular forms are related to one of the multicellular kingdoms. There is evidence that some unicellular taxa (e.g., the kinetoplastids, euglenoids, or ciliates) are independent lineages and not related to the multicellular organisms, and these forms should be placed in their own separate taxonomic categories. Thus, it has become clear that commonly used 5-kingdom classification schemes and traditional categories (such as zooflagellate, phytoflagellate, and sarcodine) are oversimplified and simply inadequate for describing the true nature of diversity, and that multiple kingdoms are needed.

Determining what and how many of these categories there might be is not easy (see history of the field in Lipscomb, 1991). Cladistic analyses of the ultrastructural and biochemical features of the cell (Lipscomb, 1985, 1989, 1991, in prep.) confirmed the presence of at least thirteen major groups of protists, all of which, incidentally, had been proposed individually by earlier, more traditional systematists (e.g., Smith, 1951; Jeffrey, 1971; Leedale, 1974; Edwards, 1976; Taylor, 1976, 1978).

Some of these groups have traditionally been called algae because they are photosynthetic. Algae are not all phylogenetically related. In fact, the occurrence of at least six distinct lineages of algae provides immediate evidence for their biodiversity (Andersen, 1992):

1. *Rhodophyta.* The red algae, primarily because they can be multicellular and reach large body sizes, are persistently considered to be plants by many biologists even though their biology is quite different from that of green plants. They are characterized by chloroplasts bounded by two membranes containing separate thylakoids and lacking an external coat of endoplasmic reticulum (Dodge, 1973; Pueschel, 1989). They have chlorophyll *a* , α- and ß-carotene, leutein, and zeaxanthin. Other pigments include the water-soluble allophycocyanin, phycocyanin, and phyrierythrin localized in phycobillosomes found on the thylakoids of the chloroplast. Floridean starch is the major storage product and it is found in the cytoplasm rather than the chloroplast. This carbohydrate has a primary chain of α-(1,4)-linked glucans with a 1,6-linked branched chain (Raven et al., 1990). There are no flagella, centrioles, or basal bodies (Pueschel, 1989). Without centrioles, it is not surprising to find that mitosis in red algae is different from that in green algae and

higher plants. The spindle forms on a unique nucleus associated organelle (called the NAO), which is located on each division pole. Furthermore, the nuclear membrane does not break down but remains intact except for small openings at the pole for the spindle to pass through (Scott, 1983). Red algae have the oldest fossil record of all the algae, with the bangiophytes found in 1.25-billion-year-old rocks (Butterfield et al., 1990). One cannot make too much of this because the fossil record for most early eukaryotes is very poor and some other protist group may have predated the red algae but left no record.

2. *Chlorobionts.* This clade represents one of the major groups of photosynthetic organisms. It includes the chlorophytes, charophytes, prasinophytes, and the multicellular plants. It has also been referred to as the chlorophyte series (Taylor, 1978) or the Viridiplantae (Cavalier-Smith, 1983). All of these taxa have chlorophylls *a* and *b*, and α-(1-4)-linked glucan (amylose/amylopectin) as a food storage in their chloroplasts. The chloroplast is bounded by two membranes, as in the rhodophytes, but the thylakoids are in many-layered grana. Motile cells with flagella have a stellate flagellar transition region and a cruciate flagellar root system. Most unicellular chlorobionts have a cell wall or scales, but not always made of cellulose.
3. *Cryptophytes* (= Cryptomonads) can be characterized as having chlorophyll *a* and c_2, phycobillins, and the xanthophyll alloxantin in chloroplasts surrounded by four membranes and thylakoids in stacks of two. The inner pair of membranes forms the plastid envelope and the outer pair forms the plastid endoplasmic reticulum. There is an expanded space between the plastid endoplasmic reticulum and the plastid envelope on one face. This expanded area contains ribosomes, starch grains, and the nucleomorph (a unique double membrane bound structure containing DNA). The nucleomorph has been postulated to be a vestigial nucleus belonging to a photosynthetic eukaryotic symbiont (Ludwig & Gibbs, 1987; Douglas et al., 1991). The food storage is the α-(1-4)-linked glucan glycogen, and it is stored in the nucleomorph. The mitochondrial cristae are flattened tubes. The flagella have tubular mastigonemes in two rows on one flagellum and one row on the other. They also possess a unique extrusome, called the refractile ejectosome, and a periplast of proteinaceous plates underlying the cell membrane.
4. *Chromobionts* (= Stramenopiles) are a group including both photosynthetic and heterotrophic forms. These are the heterokont unicellular organisms with tubular cristae in their mitochondria, mastigonemes in at least two rows on one of the flagella, and a ß(1-3)-linked glucan as a food storage product. Those forms that are photosynthetic have chlorophyll *a*, *c*1 and *c*2, thylakoids in stacks of three, and four membranes surrounding the chloroplast with the outermost membrane continuing around the nucleus.

The placement of the oomycete and hyphochytrid fungi and the labyrinthulids with the chromobionts is not surprising and was suggested by mycologists (e.g., Barr, 1981, 1992). They share with the Raphidophyta a similar flagellar root structure that consists of a sheet of microtubules extending over the surface of the nucleus. All these taxa share with the gamete of foraminiferans the presence of mastigonemes in two rows on the forward projecting flagellum and a naked trailing flagellum.

The heliozoan Actinopodea appear to be derived from the chromobionts, specifically from the chrysophyte order Pedinellales. The Heliozoa were traditionally considered to be sarcodines because they have pseudopodia. These pseudopods, usually called axopodia, are long and slender and are made rigid by a core of microtubules. Ultrastructurally identical structures form an anterior ring around the flagella of the Pedinellales. Thus, presence of axopodia is a synapomorphy that unites the Heliozoa with the chrysophytes. This relationship has been reported before by protozoologists (e.g., Patterson, 1989) but often ignored by phycologists.

Loosely allied with the chromobionts are the Eustigmatophyta and the bicoecids. The Eustigmatophyta are photosynthetic and, as with other chromobionts, they have four membranes surrounding their chloroplast with thylakoids in stacks of three and two rows of mastigonemes on one flagellum. However, there is only chlorophyll *a* (no *c*) and the outermost chloroplast membrane is not continuous with the nuclear membrane. Whether the eustigmatophytes are primitive chromobionts or derived forms with many secondary losses cannot be determined at this time. The colorless, phagotrophic bicoecids have been considered to be related to the chromobionts by other protistologists be-

cause they also have two rows of mastigonemes on one flagellum, and their flagellar root structure is similar to that of the gametes of brown algae and the xanthophyte *Vaucheria* (Moestrup & Thomsen, 1976). However, they have evolved many unique features that are perhaps obscuring information that would allow us to place them definitively as the sister taxon to one of these chromophyte groups.

5. *Euglenozoa.* The euglenids and the kinetoplastid flagellates were first recognized as related taxa by Leedale (1967). The morphological features these taxa share include linked microtubules underlying the cell membrane, and discoidal cristae in the mitochondria. Some members of the Euglenida (or Euglenophyta in the botanical literature) are autotrophic and possess chlorophyll *a* and *b*. It has been hypothesized that these chloroplasts are the remnants of endosymbiotic chlorobionts or chlorobiont chloroplasts (Lefort-Tran, 1981; Whatley, 1981). Like many chlorophyte chloroplasts, those of the euglenids lack light-harvesting carotenoids (Rowan, 1989) and a girdle lamella. In addition, each chloroplast is surrounded by an additional single membrane (Dodge, 1973), which is consistent with the idea that they are remnant symbionts. Euglenids have a unique storage product, paramylon, which is a ß (1,3)-linked glucan chain stored as grains in the cytoplasm. Phagotrophy is common in both photosynthetic and colorless forms, and the microtubules associated with the base of the flagella play a role in feeding (Triemer & Farmer, 1991).
6. *Alveolates.* The Dinoflagellata and Ciliophora have been linked as sister taxa on the basis of an alveolar membrane system and the presence of microtubules lining the cytopharynx. Because they also have alveolar membranes, the parasitic Apicomplexa are also included in this lineage. This alveolar membrane system consists of a layer of membrane-bound sacs lying just beneath the plasma membrane. In the dinoflagellates, these alveoli contain the theca. Some dinoflagellates are photosynthetic and so are sometimes called algae. These photosynthetic forms contain chlorophyll *a* and c_2 complexed with a unique xanthophyll, peridinin.

The Ciliophora make up one of the largest groups of protists and, as has already been discussed, play a major role in microbial food webs as predators and bactivorous organisms. Ciliates generally have rows of cilia with a unique system of two microtubular and one fibrous roots. They also possess two kinds of nuclei: a micronucleus that functions in genetic exchange, and a macronucleus that functions in protein synthesis.

The Apicomplexa are all symbiotic and include many major disease-causing organisms (e.g., *Plasmodium,* which causes malaria). The anterior end of the cell contains a unique complex of organelles that presumably function in attachment and penetration of the hosts' cells.

The remaining groups consist almost exclusively of heterotrophic organisms. Many of these have been called protozoa, but this shared mode of nutrition is not sufficient to unite all of these forms into a taxonomic category.

7. *Parabasalida.* These heterotrophic flagellates all possess a distinctive flagellar root structure, which includes a rod of microtubules that extends from the basal bodies around the surface of the nucleus (= axostyle). An elaborate stack of golgi vesicles is often associated with this root between the nucleus and the basal bodies. These protists are almost exclusively symbiotic and are found in many different hosts. Some species, such as *Trichomonas,* are parasites of humans, but other species, such as *Barbulanympha* and *Trichonympha,* inhabit termites and the woodroach *Cryptocercus* where they aid in the digestion of cellulose.
8. *Metamonadida.* The majority of these flagellated protists are intestinal symbionts (e.g., *Giardia*), but some are free-living. They were once thought to be closely related to the parabasalans with whom they share the absence of mitochondria and storage glycogen, but they lack the axostyle and golgi apparatus. The metamonads are characterized by the presence of three bands of microtubules associated with the base of their flagella: a supranuclear band, an infranuclear band, and a band paralleling the recurrent flagellum and oral inpocketing.
9. *Animals.* The taxa that are included in the animal clade are all united by mitosis in which the nuclear membrane breaks down by fragmentation, septate junctions, choanocytes, collagen, spermatozoa, and basal bodies at right angles to each other in flagellated cells. Grouping with the animal taxa are a protozoan taxon (the choanoflagellates) and the Chytridiomycota (chrytid fungi). The chytrids are grouped with the sponges and choanoflagellates because all have microtubules radiating perpendicularly to the basal body, which are interconnected by concentric rings of electron-

dense material (Lipscomb, 1989, 1991; Barr, 1992).

Although additional data is needed to be certain, it is probable that the Myxozoa, a group of protists with multicellular spores and specialized structures called polar capsules, will belong to the animal lineage. Like the true metazoans, they have a separation of somatic and germ cells and cell junctions. The polar capsules share many striking characteristics with the nematocysts of cnidarians (Lom, 1990), and these similarities appear to be synapomorphies that unite the Myxozoa with the cnidarian clade.

10. *Amoeboflagellates.* The amoeboflagellates and the cellular slime molds form a clade in which the taxa form limax amoeba that move relatively rapidly by the production of eruptive pseudopodia that lack fine extensions. This relationship has been suggested by other protozoologists (Page, 1976). The amoeboflagellates are also able to transform to a flagellated stage.
11. *Rhizopods.* The rhizopods with blunt lobose pseudopodia can be only tentatively grouped together. They have a simple cell structure and lack many of the characteristics used in the cladistic analysis. As the analysis is expanded, we may discover that this group is polyphyletic.
12. *Opalinids and Proteromonads.* These possess similar arrays of subpellicular microtubules underlying the folds in their cell membranes and a unique form of pinocytotic heterotrophy. Mignot (cited in the paper by Brugerolle & Joyon, 1975) was the first protozoologist to suggest that these forms were related.
13. *Microsporidia.* The members of this group have a number of features that are not apparently homologous to features found in other protists. They are small (2–7 μm) intracellular parasites that infect many kinds of eukaryotes, including other protists. The spore is the developmental stage with the longest duration, and at the light microscopic level it is the only life cycle stage that can be identified as belonging to a microsporidium. Not surprisingly then, most of our morphological information comes from the spore stage, which has a characteristic polar tube and cap used to inject sporoplasm into a host cell where it can grow and divide. Phylogenetic analysis of the small subunit rRNA often shows the microsporidians diverging first off of the eukaryote tree. This is most conservatively interpreted as meaning that the microsporidians are unique eukaryotes well adapted to intracellular parasitism. But some have interpreted this to mean that the microsporidians are direct descendants of primitive eukaryotes (e.g., Cavalier-Smith, 1993).

In conclusion, a new classification consisting of at least 13 groups of eukaryotes is emerging, but a robust phylogeny of the eukaryotes will not be resolved until more taxa are examined with both morphological and molecular techniques. First, cell biology, particularly electron microscopy, has provided the basic data on which this multi-kingdom system is based, and many of these characters turn out to be convergent, or reversed, or both. For this reason, some branches are defined by very few characters and cladograms have several unresolved branch points where several lineages appear to diverge simultaneously rather than form a more informative branching pattern. Second, analyses do not yet include many parasitic and structurally unique forms. Thus they do not address phylogenetic placement of all of the taxa.

Conclusion

An appreciation and understanding of the natural world depends on a description of the systematic and ecological diversity of microorganisms as well as the better-known plants, animals, and fungi. There can be little doubt that the biodiversity of microorganisms is still poorly known. Yet as our knowledge has grown it has become increasingly clear that these organisms are an essential and diverse part of the ecosystems of the world.

There is no consensus on the phylogenetic relationships of the various unicellular organisms at the phylum and kingdom level and, as long as new taxa and characters are discovered, innovations in classifications of the kingdoms will likely continue. It is obvious that classifications that divide organisms into just two, three, four, or five kingdoms are too simplistic, and a multi-kingdom system provides a more realistic view of the diversity of life. Concomitant with this is the realization that some traditional categories such as monera, algae, protozoa, or fungi can no longer be considered distinct phylogenetic groups. An overall scheme of classification that reflects our growing databases has not yet completely emerged. Undoubtedly, it will not resemble those followed in many textbooks today, but it will reflect more accurately the relationships of the unicellular microorganisms.

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AN INTERNATIONAL VIEW OF NATIONAL BIOLOGICAL SURVEYS[1]

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Abstract

Museums and herbaria in industrialized countries hold a huge amount of data in the form of labels associated with specimens collected in developing countries. These data represent a significant part of the existing information on biodiversity available for most developing countries. In this paper we first discuss the usefulness of the label information, providing some examples from Mexico. Acquiring and updating the information requires international cooperation, including the agreement of common policies for ownership and use of the data. Beneficiaries of such efforts will be not only the countries that assemble the databases from foreign museums, but the international scientific community as well, due to the increased scientific value that large databases coupled with modern computer technologies provide.

Surveying the biological diversity of a nation involves the inventorying, cataloging, and mapping of ecosystems, species, populations, and genes. It may also include research on the dynamic aspects of population biology, community and ecosystems ecology, and human uses of the different components of biodiversity. The task of biological surveying is among the oldest that biologists have faced (Badiano, 1552; Hernández, 1790). However, the increasing rate of ecosystem destruction with its associated species extinction and genetic erosion (McNeely et al., 1990; Wilson, 1992; Ehrlich, 1995; Whitmore & Sayer, 1992), and the realization that perhaps 90% of the species on the planet remain to be named, not to mention mapped or understood (May, 1990; Groombridge, 1992; Stork, 1988), have added urgency to the problem. To address this urgency, new methods of documenting biodiversity are currently being developed—such as Rapid Assessment Programs (RAPs) (Conservation International, 1991, 1992, 1993a–c), the division of labor and information management methods of Costa Rica's Instituto Nacional de Biodiversidad (INBio) (Janzen et al., 1993), All Taxa Biotic Inventories (Janzen, 1993), new sampling methods including the so-called BioRaps (Margules & Austin, 1995), where extrapolations of distributions are obtained prior to the sampling (Margules & Redhead, 1995), and advanced methods using sensors and pattern recognition software.

The reasons different societies and cultures may have for cataloging biodiversity run the spectrum from the strictly utilitarian to the philosophical and religious (Norton, 1987; Wilson, 1992). In countries like Mexico, which has a large, diverse rural population (Sarukhán et al., 1996), utilitarian reasons are very important. Indeed, in Mexico more than 3000 species are used as medicinal plants (Argueta et al., 1994), many other species have industrial applications (Sarukhán & Dirzo, 1992), such as jojoba for high-grade oil, and there are hundreds of varieties of corn, beans, chile, and other species that are used for food. Still, non-utilitarian reasons for preserving biological diversity are expressed very forcefully by different segments of the public, such as outcries for protecting the monarch butterfly [Secretaría de Desarrollo Social (SEDESOL), 1993], waterfowl [Commission for Environmental Cooperation (CEC), 1995], marine mammals (Salinas & Ladrón de Guevara, 1993), and other conspicuous species. A good example in plants is the recently discovered *Lacandonia schismatica* (Martínez & Ramos, 1989), which despite being apparently useless and inconspicuous has been protected by the Chole Indian community of San Javier, Chiapas, at the cost of not clearing the remaining patch-

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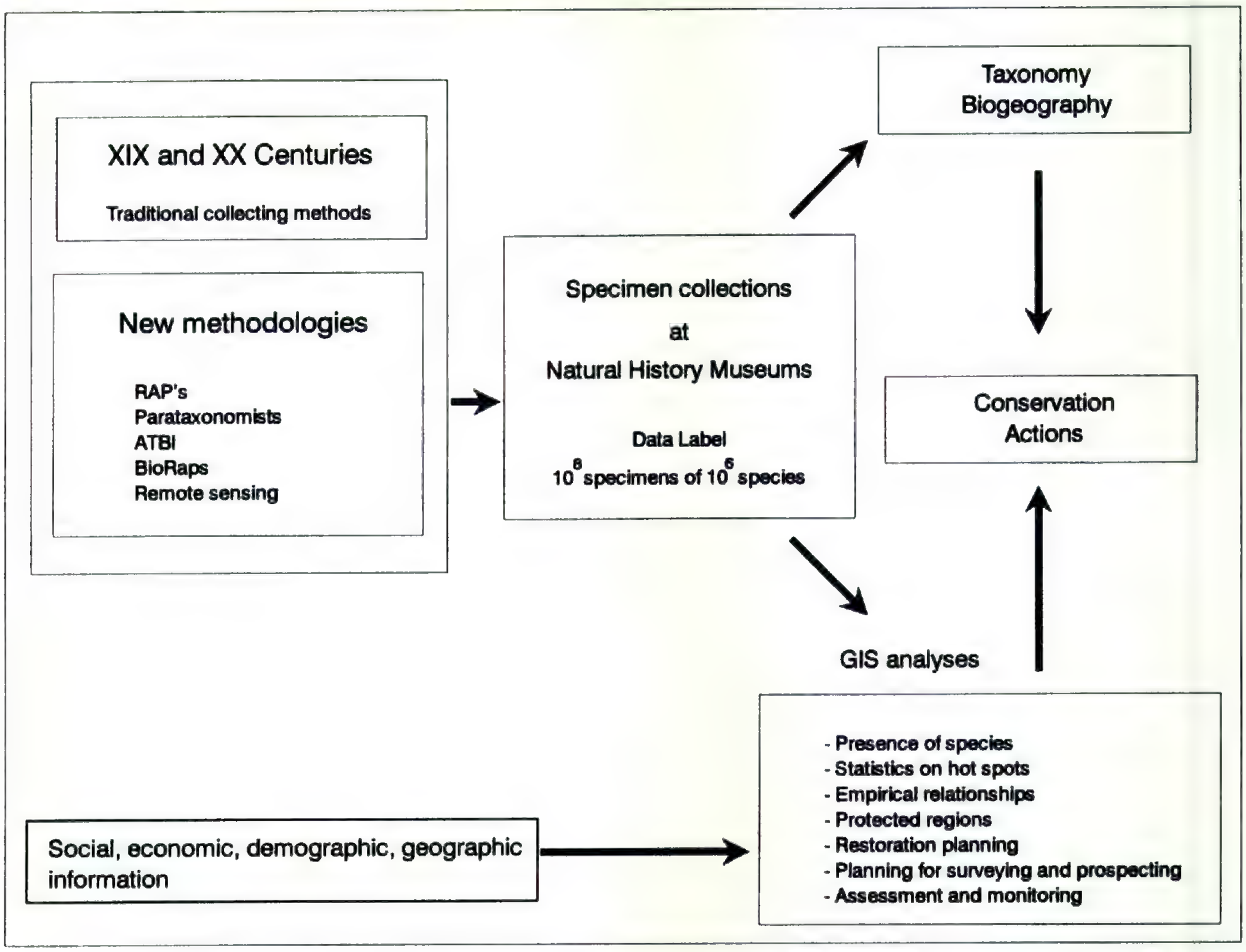

Figure 1. Traditional and new methods of collecting provide information about presence of species, mostly as labels on specimens. This information may ultimately have practical applications for conservation, alone or coupled with other types of data.

es of rainforest where the first population was discovered (Coello et al., 1993).

There is no doubt, then, that both in developed and underdeveloped countries different segments of the public, for different reasons, desire to preserve or sustainably use biodiversity. Consequently, governments have begun to design national programs for surveying biological diversity [National Research Council (NRC), 1993; Maddox & Gee, 1994; Gámez et al., 1993; Environmental Resources Information Network (ERIN), http://www.erin.gov.au/general/], and to create multinational agencies or agreements that support or encourage such efforts (e.g., Global Environment Facility, Convention of Biological Diversity).

In this paper we will concentrate on surveying species from the point of view of the Mexican biodiversity agency, the Comisión Nacional de Biodiversidad (CONABIO). First, we will present arguments for inventorying existing collections and exploring the possible uses of the specimen label data. Second, we will describe our experiences and points of view on the role that foreign institutions play in such efforts. Third and finally, we will illustrate these two points using specific examples from CONABIO databases.

The Usefulness of Label Data

During the last two centuries major efforts were made to explore, collect, and inventory the natural world. Museums and collections are the depositories of the results, and it is because of the existence of the specimens located in those depositories that organized biological studies are possible (Janzen, 1993; Wheeler, 1995).

The museums and herbaria of the world hold in the order of 10^8 specimens of an order of magnitude of about 10^6 species (Chalmers, 1996), collected in localities that, to a certain gross spatial scale, cover most of the surface of the planet and an important part of its waters. Therefore, the information these specimens provide should represent the base for national inventories. However, for most of these specimens, we know little more than the date, location, collector, and name, and much of this in-

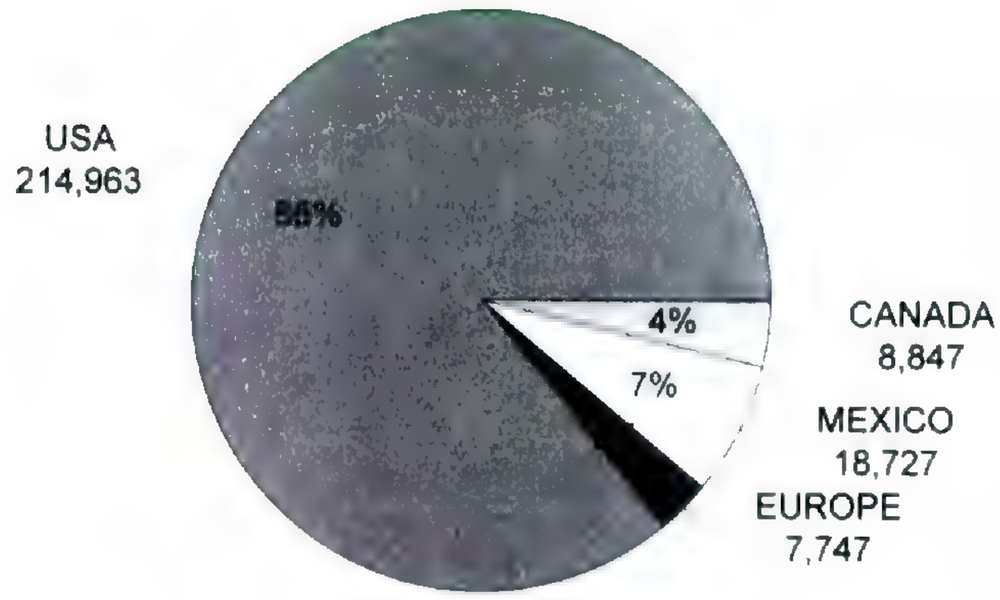

Figure 2. Graphic representation of the Bird Atlas of Mexico database showing the proportions of Mexican specimens that are housed in collections in different countries.

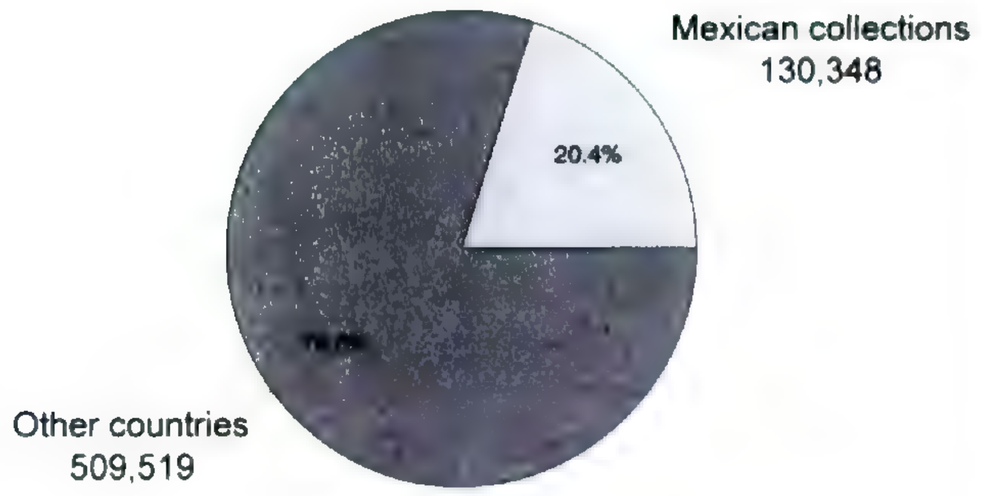

Figure 3. Graphic representation of CONABIO's all-species databases showing the proportions of Mexican specimens housed in collections in different countries.

formation has some degree of uncertainty, both taxonomic and geographic. One obvious question is what use such apparently meager data has for conservation biology. Despite the serious limitations, such data have constituted the basis for much of classical biogeography, and it is the common ground where systematics, biogeography, and ecology come together to contribute to conservation biology (Fig. 1).

From the viewpoint of conservation biology, the basic results that label data from museums produce are lists of taxa and the distribution areas of taxa. Both types of biogeographical information are essential to the practical applications of conservation policies. In many countries, choosing areas to be preserved or finding locations of certain important species are the most common "scientific" tasks for conservationists (not to mention the economic, social, and political actions that in the end are the *sine qua non* of conservation).

In countries with high alpha and beta diversities but with a lack of knowledge about that diversity, having reliable lists and ways of extrapolating data from a collection locality to a larger area allow, among other things, the following:

(1) For a given site, determination of the likely presence of endemic, protected, scientifically interesting or economically important species (Bojórquez et al., 1995).

(2) Obtaining important statistics such as number of species and percentage of endemics. This also allows the location and mapping of hot and cold spots for better ecological planning (Prendergast et al., 1993; International Council for Bird Preservation, 1992; Nelson et al., 1990).

(3) Development of empirical relations between the above and easily measured climatic, geologic, and biological parameters to allow extrapolation (Margules & Austin, 1995; Margules & Redhead, 1995; Butterfield et al., 1994).

(4) Restoration planning using historical records or empirical rules for hypothetical distribution areas (Allen & Wilson, 1991).

(5) Efficient planning of surveying and prospecting, both for areas lacking previous fieldwork using "hypothetical species lists" and for species of scientific or economic interest (Margules & Redhead, 1995; Sittenfeld & Gámez, 1993).

(6) Assessment and monitoring of global climate effects on the areas of species distributions (Chapman & Busby, 1994).

Despite their usefulness, floristic and faunistic studies, and the development of procedures for the production of reliable distributional areas, have been the subject of far less theoretical and methodological development than other approaches such as, e.g., the population biological methods that underlie Minimum Viable Population Analysis (Soulé, 1987), and which are, at least in many underdeveloped countries, often far removed from the actual practice of conservation. There is no doubt, however, that the proper use of the huge amount of existing label information, in conjunction with modern computer systems, introduces many methodological and even theoretical issues, some of which we will discuss below, and therefore this should be an area of active research.

Of course, any information coming from museums, even assuming it is taxonomically adequate, may require field corroboration and is not a substitute for detailed ecological studies. But label information, because of the sheer abundance of it, its

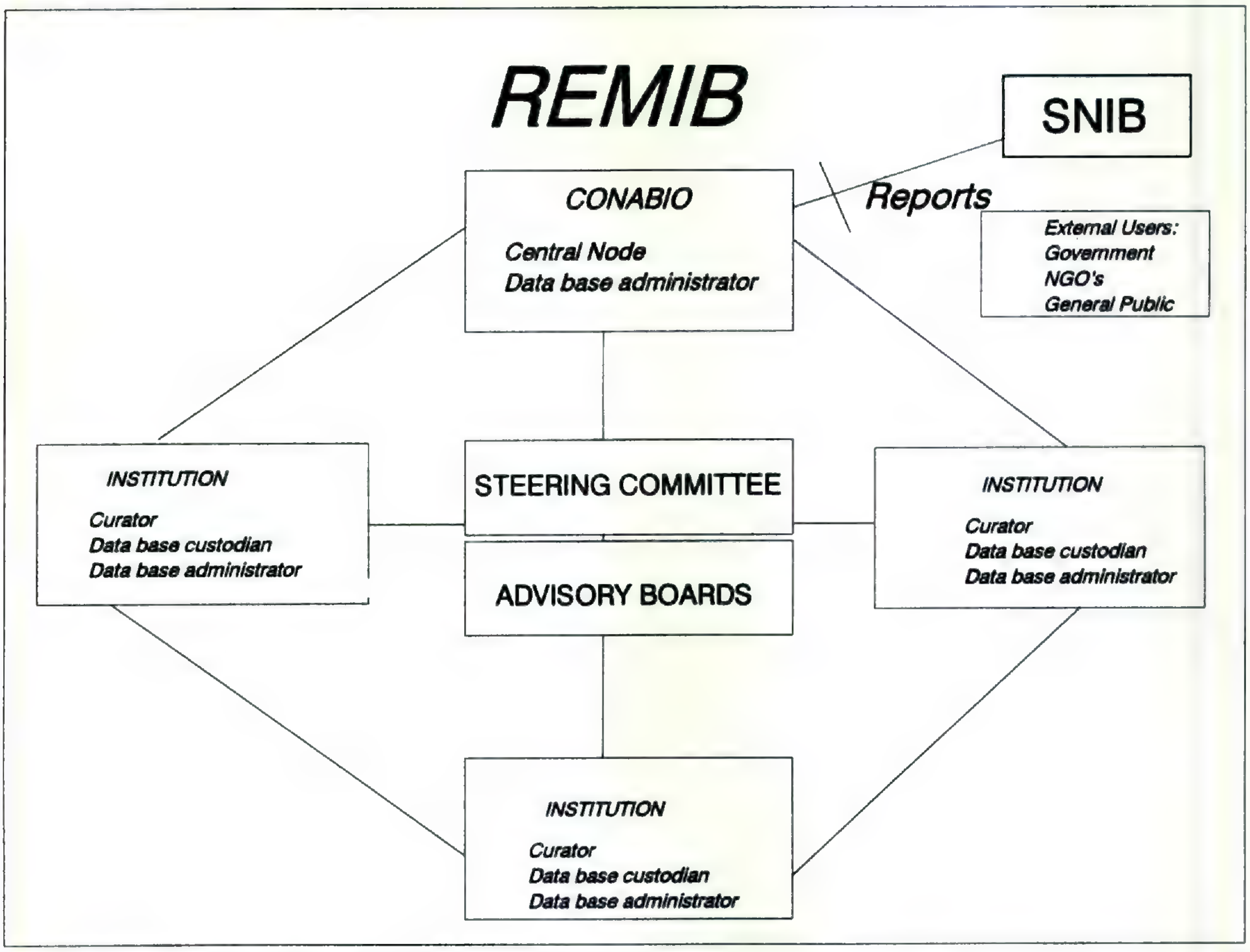

Figure 4. Structure of the Mexican network of biodiversity information (REMIB). The steering committee and advisory boards are academic bodies in charge of overseeing standards and membership to the network. SNIB is the national system of biodiversity information. The function of REMIB is to provide a mechanism for updating information maintained in the different institutions.

historical importance, and its direct relevance to important conservation questions, should have high priority in any national biological survey.

Surveying the Museums of the World

In this section we will rely heavily on the experiences of CONABIO that we believe are most amenable to generalization. Although CONABIO has supported a certain number of field studies, mainly on protected areas, and a pilot parataxonomist program, modeled on the experience of INBio, has been started, most of the efforts have been directed toward computerization of national collections and sharing information with foreign collections.

When CONABIO was created, its main objective was to promote the inventorying of Mexican biodiversity in computer data banks that could be updated regularly. There are several problems in fulfilling this task: (1) Clearly, to inventory all species inhabiting the Mexican territory is a task for generations. Priorities must be set. (2) Most of the specimens that have been collected in Mexico, with the exception of plants, are not held in Mexican collections. Sharing of data is necessary. (3) Gathering and updating the data are tasks for professional (or, in some cases, advanced amateur) taxonomists working in museums and herbaria. Policies and methods for determining the quality of data, acceptance and rejection criteria, accessing and updating the information, ownership, copyrights, economic compensation, etc., should be agreed upon between taxonomists and their institutions. (4) The size and distribution of the data make its capture in electronic formats expensive and time-consuming, requiring long-term commitments. (5) Given the dynamic and complex nature of taxonomic information and the lack of accepted standards for a taxonomic "data model," the creation of a suitable computer system was not trivial. (6) In order to be useful to a heterogeneous public—including government officers, scientists, members of non-governmental organizations (NGOs), and perhaps the general public—statistical, analyti-

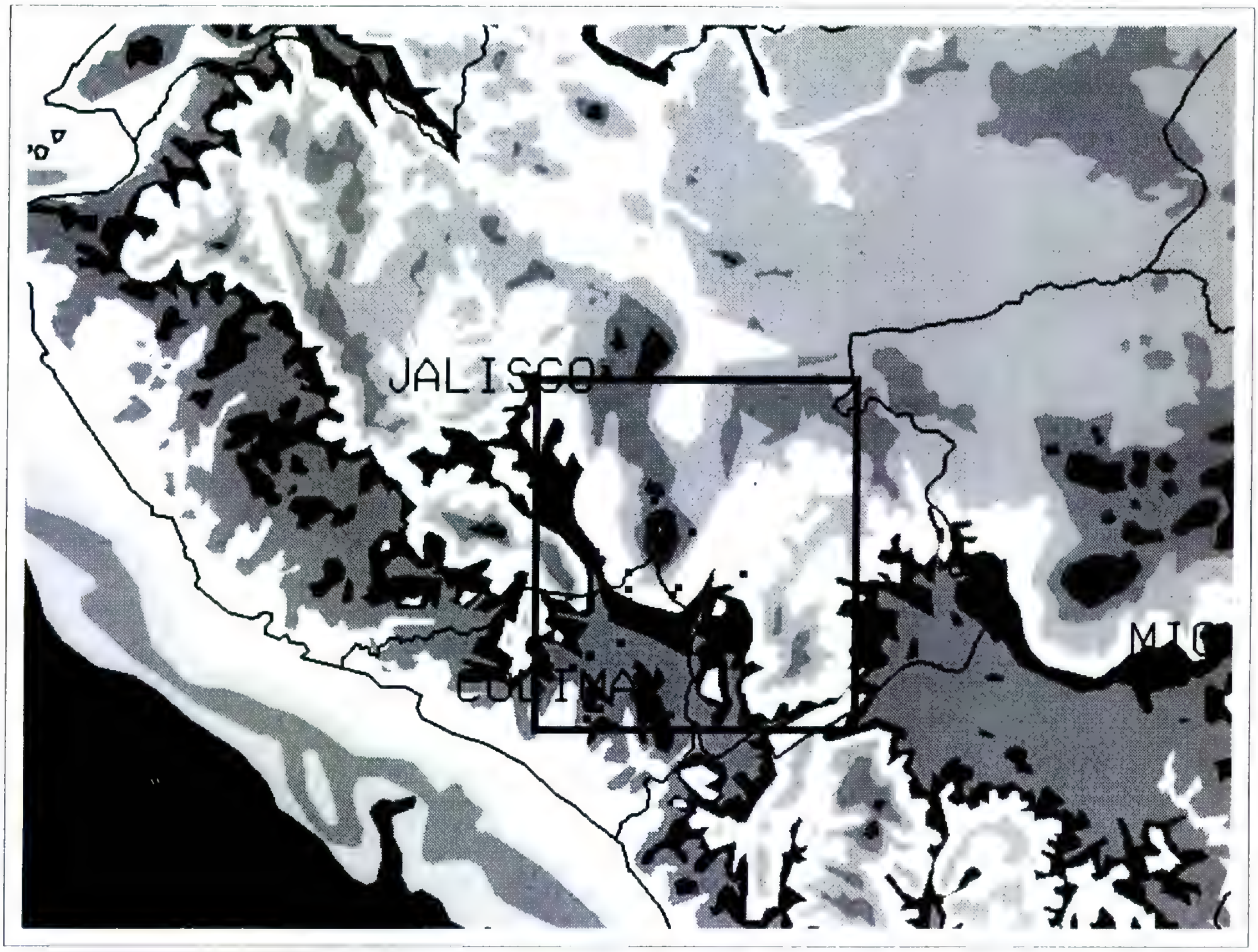

Figure 5. Distribution of collecting localities of two families of butterflies (Papilionidae and Pieridae) in a one degree per side square of the Pacific Coast of Mexico. The dots represent collection sites, and the shadings categories of altitude over sea level. Most collecting has been restricted to a limited range of altitude, suggesting that the sampling of ecological conditions is insufficient. The database used is the Butterflies Database of the Zoology Museum, School of Sciences, National University of Mexico.

cal, and display tools that help to organize the data in user-friendly and interesting ways should be devised and implemented.

SETTING PRIORITIES

Setting taxonomic and geographic priorities for the biological inventories was intensely discussed by CONABIO and its advisors. The final, pragmatic option we chose was to support work on groups in which Mexican experts were willing to work, or where there were ample and easily available data. In a second stage, results of these discussions will be used to pinpoint areas of both taxonomic and geographic ignorance. This leads many of the grants from CONABIO to be oriented toward vertebrates (terrestrial and aquatic), butterflies, some beetle families, and other important invertebrate groups, like certain families of parasitoid wasps and mollusks and annelids. The first results of those projects are now being used to plan field trips to fill in gaps, as will be described below.

SHARING INFORMATION WITH FOREIGN INSTITUTIONS

It is well known that many countries with great biological diversity do not house the best collections of their own flora and fauna. For example, about 90% of the bird specimens collected in Mexico are housed in foreign museums, mostly in the United States, Canada, and the United Kingdom (see Fig. 2). This is the case for almost any group considered at higher taxonomic categories, with the exception of vascular plants, for which there are two very large Mexican collections and several medium-sized ones. CONABIO is supporting the work of Mexican taxonomists to obtain information from the labels of specimens housed in foreign collections. In fact, by September 1995 almost 80% of CONABIO's data bank came from specimens housed in foreign collections (Fig. 3). To obtain the information a variety of procedures are used, from requesting computerized catalogs from curators to manually recording the information attached to each specimen. In this way, in the last two years

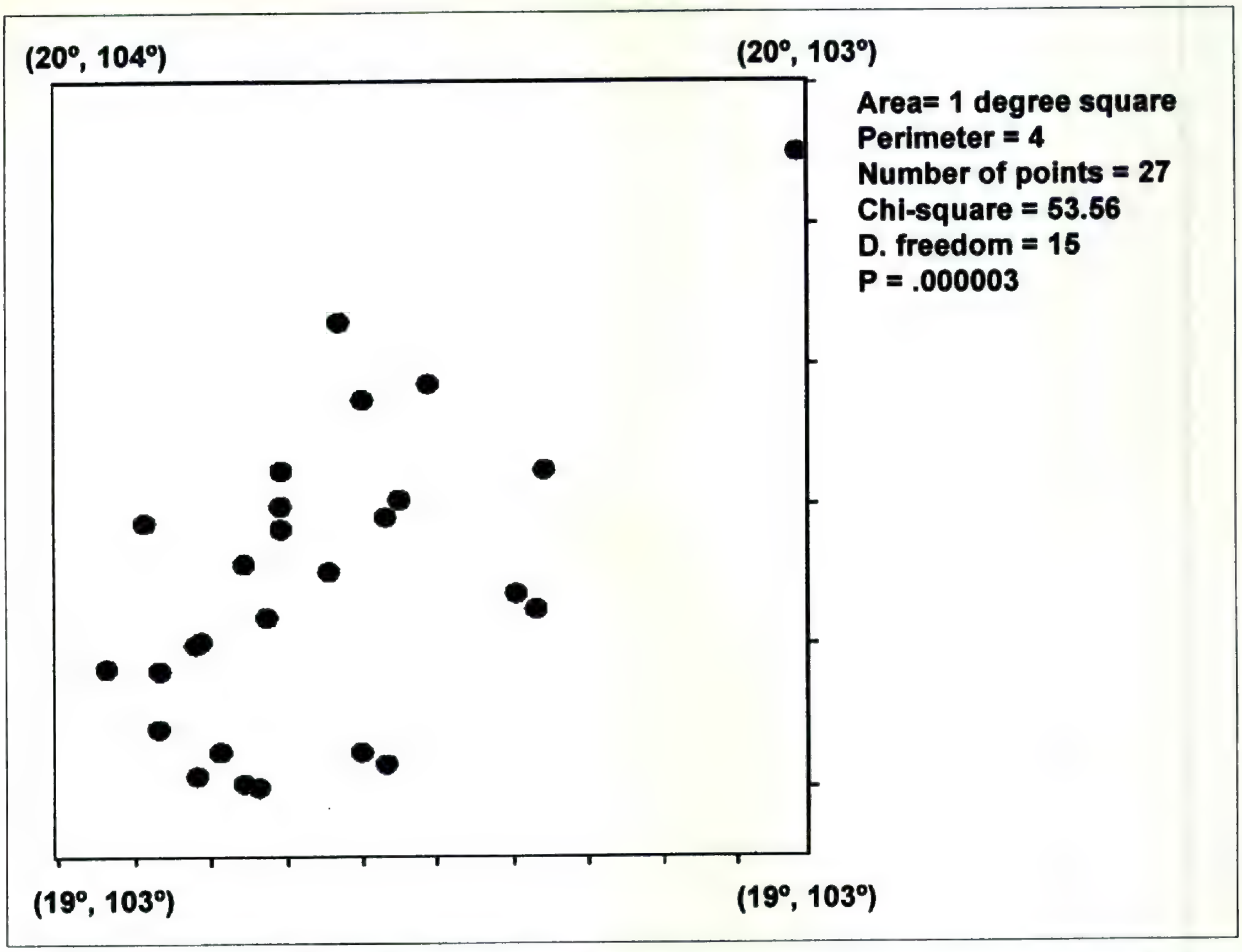

Figure 6. Spatial analyses of the data from Figure 5. Spatial distribution was analyzed for randomness of pattern, using standard techniques (see text). The null hypothesis of a random distribution of localities within the square was rejected.

information on hundreds of thousands of specimens, mostly of vertebrates and butterflies, have been assembled in databases now kept in some Mexican institutions, and eventually most of the information will be available through the Internet, via CONABIO's home-page.

Several interesting points can be learned from CONABIO's experience. When the work is done by taxonomists acquainted with the proper handling of collections, almost all foreign museums have been open to and helpful with the effort of computerizing labels. Among other things, this sometimes benefits the museums that lack computerized catalogs or the resources to computerize large collections. However, there were a number of concerns related to the idea as a whole. Most concerns of providers are associated with the precise conditions for releasing information to the public domain. In many cases this issue has been resolved by carefully stating the rights of the providers following ideas already used by the Australian Environmental Resources Information Network (ERIN), or contained in the published Association for Scientific Collections' (ASC, 1993) "Guidelines for Institutional Database Policies." These points can be formalized by signing letters of agreement or Memoranda of Understanding between the national biodiversity agency and the foreign museum. In our case, CONABIO has already signed a Memorandum of Understanding with the British Museum of Natural History, and is working on other such agreements.

POLICIES ABOUT OWNERSHIP AND UPDATING

Ownership of information is a subject closely related to the above. Although who is the "owner" of information in a public museum is open to discussion, there is no doubt that the museums, the curators of the collections, and the taxonomic experts are the actors directly involved in creating and updating the information, and they should be the authorities on the use of it. CONABIO is following the experience of ERIN regarding the concept of custodianship of the information. This means that we agree that only the providers of the databases and the curators of the collections have the authority to

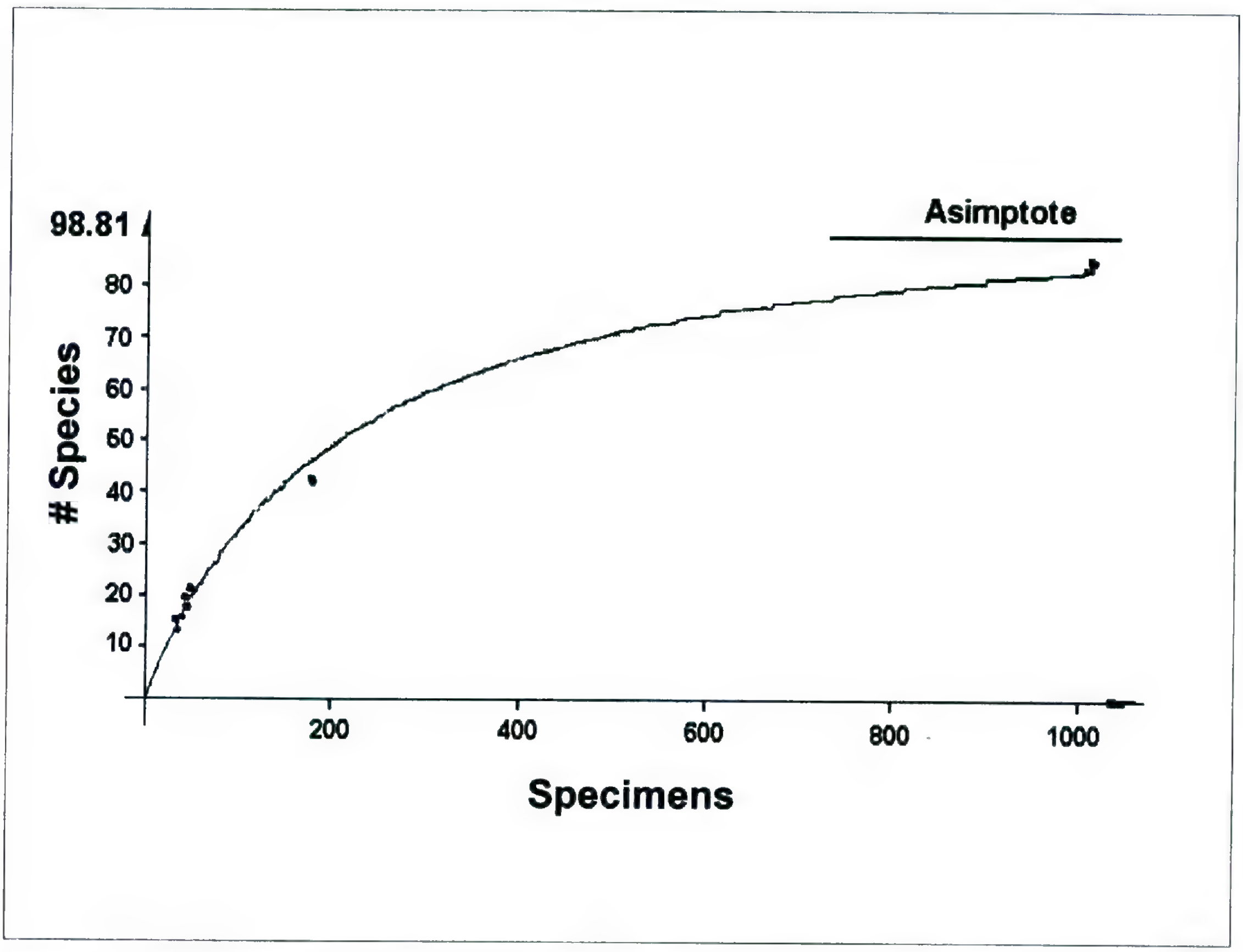

Figure 7. Species-effort analyses of the data from Figure 6. Using CONABIO's database, an accumulation of number of new species plotted as a function of collecting effort (number of specimens in five-year intervals) was done. The curve shows that for the area sampled there is a decreasing rate of new registers, and the asymptote of the curve (about 99 species) is near the last value of different species (86) collected in the area. See text for further explanation.

modify the databases. It also means that if part of the information is regarded as sensitive (for example, precise georeferencing of populations of commercially valuable endangered species) or not yet ready to use by non-experts (for example, if it is not stable taxonomically), the providers or curators have the authority to mark the fields or records as access-restricted.

CONABIO, as well as some other national biodiversity agencies (INBio, ERIN), supports a policy of open access to most of the basic information on biodiversity, that is, the label data. However, this is not universally agreed upon, and therefore before releasing any information to the public domain the formal agreements and permits should state at least what parts of the information are considered open, the disclaimers and pointers in the databases that identify the original sources and dates of the information, the responsibility (or lack thereof) of the sources, the procedures to report to the sources the amount of use of their information, and any updating mechanisms for the database.

The periodic updating of databases containing label data from many tens of thousands of specimens located in dozens of institutions in many countries is not a simple task. However, the existence of the Internet makes the task feasible. Pioneering efforts are already under way by many institutions that are making their catalogs available on-line through the World Wide Web. Among the many entry points, Cornell University Biodiversity and Biological Collections is a useful one. (Its URL is: http://muse.bio.cornell.edu.) Nevertheless, a truly distributed database of museum information is still lacking. A major international effort will be required to reach this goal (Systematics Agenda 2000, 1994).

In Mexico, CONABIO is coordinating a network of institutions in an effort called Red Mexicana de Información sobre Biodiversidad (REMIB), in which the partner institutions will have access to the information held in each collection using widely available Internet navigators. Although short of full interoperability of the databases, this will allow the

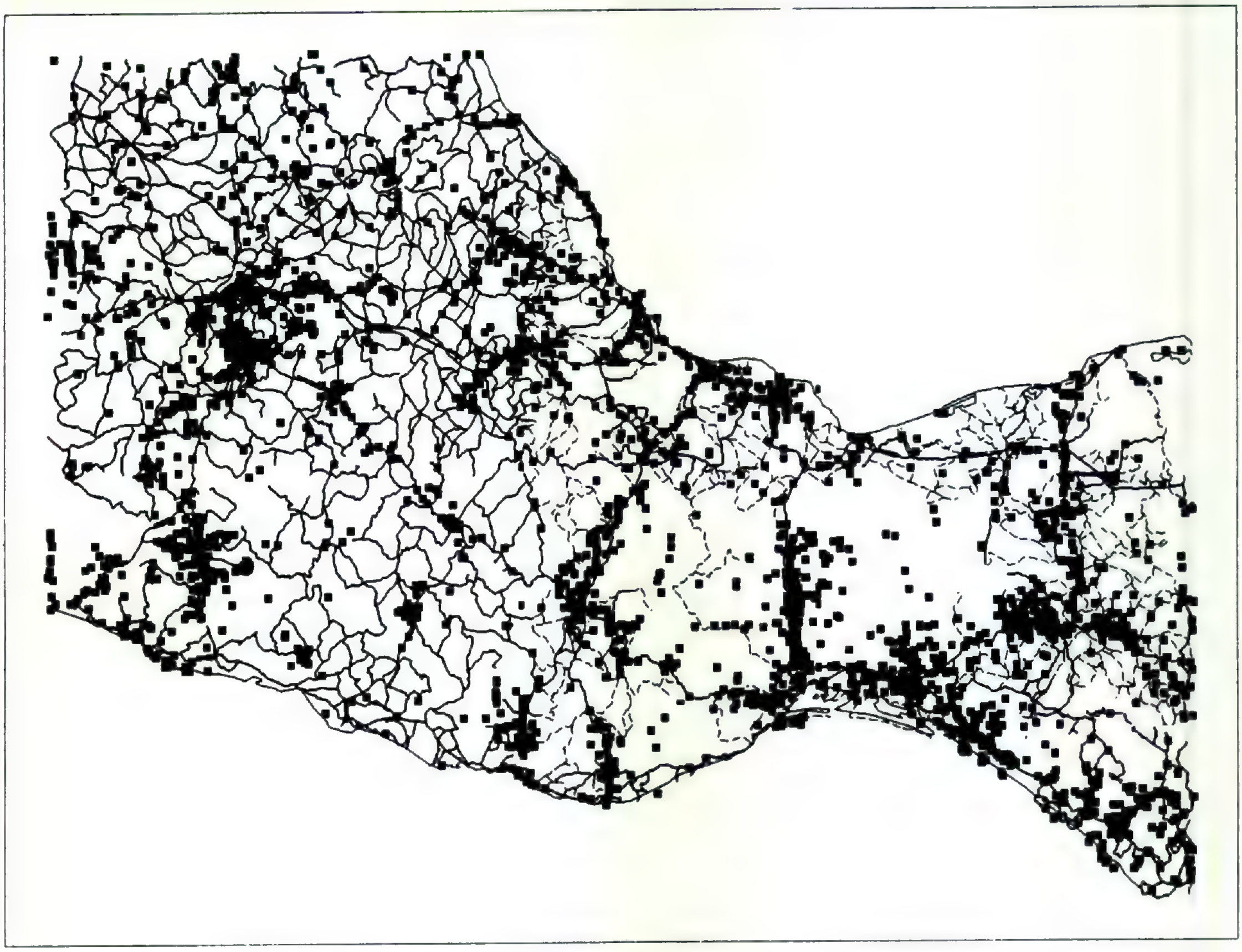

Figure 8. Dots represent collecting points in the Bird Atlas of Mexico database, near the Isthmus of Tehuantepec, in southern Mexico. Lines are roads. The figure displays the "Collector's Syndrome," in which dots tend to accumulate along roads or around biological stations.

partners to retrieve information on-line and to gain experience with the problems of creating a distributed database (Fig. 4).

LONG-TERM COMMITMENTS

Any country that attempts to create national inventories must be prepared to make a long-term commitment. Not only are lists incomplete even for vertebrates, but the detailed georeferencing required for modern studies (Margules & Redhead, 1995) is available only for certain groups or in a few countries. In the developing world, this will require the creation and strengthening of national capacities in terms of physical and human infrastructure (at the technical, professional, and research levels) to do conventional exploring and taxonomic work, but since most of the already existing data are based in museums in the developed countries, some new commitments are required. As an example, we can take the Birds of Mexico database that was compiled by A. Navarro and H. Benítez of the Museo Alfonso L. Herrera, at the School of Sciences of the National University of Mexico, and Townsend Peterson, of Kansas University. This database took more than five years and visits to 40 museums in seven countries to be assembled. The georeferencing of the locations has been going on for three years, and the debugging of the geographical fields alone has involved some 30,000 of the total 280,000 records. Maintaining and updating this database will be a permanent task that may require a budget to allow for trained personnel, traveling, computer resources, etc. Because scientific grants are difficult to obtain for these efforts, governments may have to allocate money specifically for the compilation and maintenance of these databases. All the other databases of a national scope that CONABIO is supporting (mammals, fishes, reptiles and amphibians, butterflies, and scarabeid beetles) have taken many years to be compiled and georeferenced and will require continuous efforts by their custodians at universities to maintain, debug, and update. This effort will cost resources and institutional commitments at national and international levels.

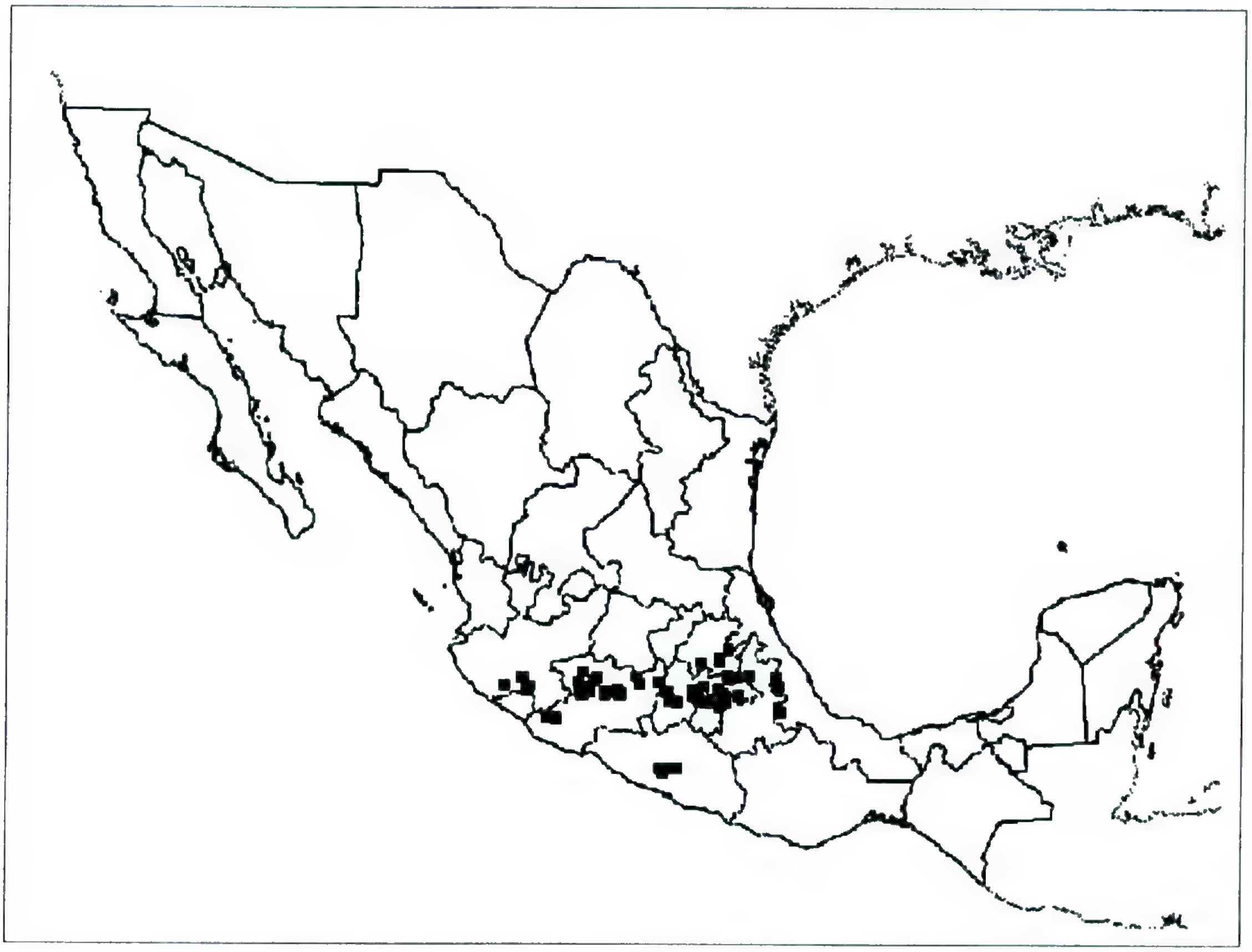

Figure 9. Collecting localities for *Abies religiosa*. Data are from herbarium specimens deposited at the Instituto Nacional de Investigaciones Agropecuarias y Forestales (INIFAP).

The commitment also means participating in the many international forums that deal with this subject. Since the issue of sharing and updating collections information on a global scale has presented a great many questions, it is important that many opinions and points of view be taken into account when agreeing on policies, standards, methods, etc. Currently, there are several more or less international efforts addressing these problems, groups like the International Organization for Plant Information (IOPI), the Working Group on Taxonomic Databases (TDWG), the International Union for Biological Sciences' group DIVERSITAS, and initiatives like Systematics Agenda 2000, Species 2000, and the Clearing House of the Biological Diversity Convention. Regular participation from member countries is needed in order to maintain an institutional memory.

DESIGN OF A DATA MODEL

To date, there is no single agreed-upon data model that can be used for an effective exchange of information among data holders around the world. This is an important subject to confront if we are to exchange and update information from different sources efficiently and consistently.

Several data models are in use in institutions around the world, for example, the databases MUSE (http://muse.bio.cornell.edu/), SMASCH (http://ucjeps.berkeley.edu/smasch.html), and TROPICOS (http://www.mobot.org/MOBOT/research/datamodel.html) and others accessible through the Biodiversity and Biological Collections Home page (http://muse.bio.cornell.edu/). However, this effort is not complete, and becomes even more complicated when other themes are added to the purely taxonomic information. CONABIO has dedicated significant time, money, and human resources to define a data model that can adequately address the diverse needs of government institutions dealing with the manifold aspects associated with biological information.

In many cases incompatible data formats among museums highlight the additional standardization effort that is required to be able to use information

Figure 10. Data on altitude, precipitation, and average yearly temperature were obtained for the collecting localities in the previous figure. The geographical information system was then used to plot other localities with similar conditions (see text).

from different sources. Taxonomists and scientific societies throughout the world must participate more actively in order to propose and enforce more effective "standards" for taxonomic information, since curatorial information represents the "core" of any biodiversity information system.

ANALYTICAL TOOLS

Amassing large databases of label information requires the development of many tools for its analysis. This includes, first, display and exploratory tools. Since the information and its interpretation are basically geographical, Geographical Information Systems (GIS) are an essential tool for displaying and organizing the data. However, due to large gaps of knowledge, inferential and predictive tools are also needed. Given the non-randomness of these samples (in space, time, and taxa), and the fact that most label information is just *presence* data, this presents some interesting statistical problems.

As an example of display tools, in Figure 5 we present the distribution of collecting localities of Papilionid and Pierid butterflies (the database comes from 15 museums in Mexico, the United States, Canada, and Europe) in a one degree per side square on the Pacific Coast of Mexico. At a glance one can tell that most of the highlands are not well sampled. An analysis of the randomness of the spatial distribution (Pielou, 1969) confirms that the points are far from being randomly distributed (Fig. 6). In Figure 7 an accumulation curve (Soberón & Llorente, 1993) is displayed. This curve shows that the effort concentrated on the area covered by the points has resulted in a significant drop in the discovery of new species. The two exploratory tools show that although the lowlands in the square may be adequately sampled, more effort is required in sampling other areas.

In another example, in Figure 8 we show the collecting localities for birds in Mexico. The map clearly displays the artifactual pattern created by overcollecting along roads or near biological stations and points out gaps where few or no collecting efforts have been made. This type of information is already being used by CONABIO to evaluate the

information about location of species provided in some environmental impact assessments.

On the matter of predictive methods, empirical modeling of the presence data as a function of easily measured, climatic or physiographic variables holds great promise (Butterfield et al., 1994). In Figure 9 we display the points where the fir *Abies religiosa* has been collected, according to the data of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) herbarium in Mexico. In Figure 10 the shaded areas show regions where similar conditions of average temperature, precipitation, and elevation occur. Similar regions were defined using a boxcar method (Carpenter et al., 1993). It is quite possible that the large shaded areas may include non-reported localities for *Abies religiosa,* and perhaps for other species of *Abies* as well. Inclusion of the information of other national and foreign herbaria would lead to a much better analysis. Leaving aside the work of Soto and Gómez-Pompa (1990), empirical modeling is just beginning in Mexico, and although the Australian experience shows that the tool has predictive power, more work is needed in the mountainous regions of Mexico. The possibilities that empirical modeling opens for bioprospecting, planning, and restoration are significant. The National Reforestation Program in Mexico will be using this tool for planning their actions in the immediate future.

Conclusions

The use of label information that is currently housed in the many museums around the world will be extremely useful for ecological planning and monitoring. The ability to assemble large label databases, together with the computing tools required to analyze them, is increasing the value of collections, museums, and the work of taxonomists around the world. Besides the practical implications for prospecting for important species, restoration and reforestation, ecological planning, locating priority areas, and monitoring and evaluating environmental impact statements, the scientific applications of the databases are quite interesting. Biogeographical and ecogeographical analyses previously done on the scales of thousands of square kilometers may be refined a thousandfold. Empirical modeling should conduce to forming hypotheses and suggesting mechanisms for explaining the correlations found.

For most countries all the above requires more than just national efforts. The collaboration of museums all over the world, together with scientific societies and many multilateral agencies and programs, will be needed to computerize and distribute the information, agree on policies and standards, develop methods and techniques for analyses, and provide funds.

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THE LAST SPECIES[1]

Lorin I. Nevling[2]

Abstract

The Last Species is an effort to examine the choices that confront us today that will determine where this nation will be in the year 3000. This presentation addresses the appropriate coordinating role for the National Biological Service, its formation and evolution, and its political liabilities. The latter receives special attention because it fits into the broader national political and environmental arena. A shift in the meaning of critical words and phrases will be singled out as a primary causal agent for the current distress within the scientific community. Some practical suggestions are made on how to engage and educate elected officials and the public at large.

The sunset is bold, harsh, colored by an acrid, hot atmosphere. The waning sun fails to diminish the heat, absorbed during the long day by a blackened scorched landscape that returns it to the atmosphere with equal force as night falls. A pair of tall pink spires droop and slowly, ever so slowly, come to reside, recumbent, on the coarse sand. Although in full flower, no seeds will result for there are no pollinators except the hot wind. They are destined to dry, to wither, and to die.

What made the earth unique exists no more. The last species is gone and the earth has become only another of billions of lifeless hulks hurtling through the cosmos. Because no eyes are around to witness the final extinction, no one cares. Is this the earthly scene that we want to mark the millennium beginning in the year 3000? I think not. If you agree, then we need to examine the present state of our national affairs and take action to assure a different future.

Many of us are reasonably sure that a meteor collision with the earth caused the last great extinction. For decades, we thought the likely cause of the next major extinction event would be a nuclear war. Remarkably, that seems far less likely today. We appear to be at the beginning of the sixth great extinction, but this time the cause is of an entirely different nature. The threat is human population with its egosystem affecting virtually every ecosystem. If not now, there soon will be too many of us and too many of us doing the wrong things. The number of individuals in a species does not protect that species from extinction; we need only to consider the fate of the passenger pigeon. The United Nations projects that the world population will grow from 5.6 billion to 11 billion by the year 2045. Most of this growth will be in the developing nations. At the end of World War II there were about 55 sovereign nations—today there are 207 (Anonymous, 1995a). Of these, approximately 90 are exploiting their natural resources beyond sustainability. Political fragmentation is reflected in numerous areas of armed or political contention throughout the world, often pitting one "culture" against another. If we look at the number of dissimilar groups that exist, we should anticipate that this fragmentation and accompanying unrest will only increase.

The United States makes up approximately 4.5% of the world's population but consumes 25–30% of the resources. Meanwhile, 1.3 billion people live in dire poverty, that is, with less than $1 a day of income. Consider further what a small percentage of its budget this nation spends on research and it becomes clear why the funding of research has become increasingly difficult. The U.S. spends more than $350 billion for advertising, exceeding the gross national product of Australia. The value of our arms exports vastly exceeds that of foreign aid. Common sense dictates that we cannot continue on this path over the long term. It is imperative that we acknowledge that all commerce takes place within the parameters of our natural resources. If we fail to make this acknowledgment, and understand and appreciate the limits it places on our actions, we are doomed to self-destruction.

It is clear that the world's tropical forests are being irretrievably lost, with 69% being converted to marginal agriculture, charcoal, local use, or export to developed nations. Much of the tropical for-

[1] This paper was presented as an after-dinner address at the Garden's 42nd Annual Systematics Symposium. It was accompanied by nearly 120 slides that are not reproduced here. I am especially grateful to Michael Jeffords and James Crowder of the Illinois Natural History Survey for advice and logistical, technical, and electronic support during the preparation and delivery of this presentation.

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est is being devoted to the manufacture of plywood in some developed nations. This plywood, in turn, will be used primarily to make construction forms. Closer to home, the oak logs cut in southern Illinois are used primarily to construct pallets. We are losing a vast array of plant and animal species that will remain forever unknown.

The worldwide collapse of fisheries is a fact and is due to overexploitation, various pollution factors, and the application of ill-founded hatchery, stocking, and aquaculture practices. If you do not believe that there is a collapse, check your local market prices and species availability.

Eighty countries (Anonymous, 1995b) have moderate to severe water scarcity, and these countries are home to 40% of the world's population. The global demand for water is estimated to double every 21 years. Irrigation consumes 90% of all water used in poor countries with up to half of it being wasted. It is estimated that 10 million deaths annually are water related. Drinking-water quality is a problem even in this country with federal standards sometimes being exceeded by nitrates and the herbicide atrazine, as well as several other pesticides, in the Midwest (Taylor, 1994). For example, the regulatory level for atrazine is three parts per billion with the highest actual sample level at more than six times the regulatory level. Recent research has shown that DNA modification occurs in hamster tissue at the regulatory level, that is, at three parts per billion (Gunset, 1995).

The organism *Cryptosporidium* is scarcely monitored by water finishers even though it is an increasing problem. A check of untreated intake water in 66 water treatment plants in the U.S. identified the presence of *Cryptosporidium* in 87% of the plants (LeChevillier et al., 1991). The 1993 outbreak in Milwaukee of cryptosporidiosis is estimated to have caused 400,000 illnesses (Mac Kenzie, 1994) resulting in a loss of $37,000,000 (Smith, 1995) in unearned wages and productivity.

Given the large number of activities of the biological community that range over an absolute galaxy of interests, some centralized coordination may be necessary if we are to make overall progress in protecting the environment. What others are either unable or unwilling to do is an appropriate and logical function of government. In this case, no one has been able to function as an organizer, so it falls to the government to become the organizer and coordinator.

It might be helpful to briefly review the recent history of a biological survey for the U.S. in order to better appreciate the present political and biological situation.

- 1977. Canadian entomologists begin to plan for a Canadian National Biological Survey. Michael Kosztarab, Virginia Polytechnic Institute and State University, initiates discussions on the need for and utility of a biological survey for the U.S.
- 1982. The Association of Systematics Collections (ASC) endorses the biological survey concept and is soon followed by the endorsement of 28 other scientific societies.
- 1984. A major unscheduled discussion of the biological survey takes place at the ASC annual meeting hosted by the Illinois Natural History Survey.
- 1985. The ASC annual meeting results in the publication *Foundations for a National Biological Survey* (Kim & Knutson, 1986).
- 1986–1992. A bewildering array of meetings with federal agencies and members of Congress takes place. Legislation was drafted but never advanced. A last-minute attempt in 1992 to form the National Biological Survey (NBS) by Presidential Order failed to materialize.
- 1993. Department of the Interior Secretary Bruce Babbitt forms the NBS by Secretarial Order. He also poses a series of questions to the National Research Council (NRC) about the organization and direction the Survey should take. A 19-member committee, under the leadership of Peter Raven, was assembled and issued its report *A Biological Survey for the Nation* in October 1993. This report served as the major guideline for the development of the Survey. One of the stated reasons that Secretary Babbitt formed the Survey was to prevent "environmental train wrecks." In order to accomplish this he thought it necessary to "develop data that everyone could agree was accurate." In turn, this would lead to an increase in the quality of natural resource management decisions. In a parallel statement, Illinois Governor Jim Edgar, referring to the three Illinois surveys, stated, "Surveys play a very important role in helping us in government make better decisions because we have the facts from the Surveys."
- On February 24, 1994, the Association of Systematics Collections and the Department of the Interior entered into a Memorandum of Understanding. As a result, a Systematics Resources Working Group, consisting of representatives of ASC and NBS, together with representatives from the Environmental Protection Agency, National Marine Fisheries of the National Oceanic and Atmospheric Administration, the U.S. Department of Agriculture and, more recently, the

National Science Foundation, entered into a planning process to assist in the implementation of the MOU.

- In June 1994, Ronald Pulliam is named Director of the NBS.

Given all this orderly and logical progression of organization and activities, what changed to place us in our current circumstances, that is, attempting to defend the enforcement of environmental law?

The scientific community was so buoyed up by what we interpreted as positive trends and developments that we became complacent, even self-satisfied, and failed to recognize the controversy that had been developing for many years. The signs were there—some were even discussed at professional meetings—but we did not appreciate the depth of negative feeling toward regulation. Unfortunately, Stan Shetler (1995) may have had it right when he said, "I believe, however, that reaction to federal environmental protection and conservation efforts and the funding of science has been setting in for a long time and that the change in American attitudes about regulations and tax support is not a passing fancy."

What happened? In my opinion, the language changed. Language is a living, dynamic thing and words do change. In *Through the Looking Glass* (Carroll, 1977), "When *I* use a word," Humpty Dumpty said, in a rather scornful tone, "it means just what I choose it to mean—neither more nor less." "The question is," said Alice, "whether you *can* make words mean so many different things." The answer is yes, one can make words mean different things at different times. One technique of developing pejorative meaning in words is demonization, which is a favored format of religious and political leaders. Even a casual examination of the political debates of our time indicates that religion and politics seem to be merging with increasing frequency and ferocity.

Reversing the connotation of a word is accomplished with relative ease through the use egregious examples based on falsehoods or near-truth. Let me translate a few code-word examples: natural resource abuse = wise use; that science with which exploiters agree = good science; review by the exploiter community = peer review; obstructionist = environmentalist. "Traditional family values" also falls into this category. A little genealogical research by some zealots might convince them that their antecedents were not all that great. An example of our own making is "theory of evolution." Theory has vastly different meanings for scientists and the general public. This difference in meaning opened the door for scientific creationism. Another set of catchwords that remains confusing to the scientific community is "ecosystem management."

My father was always interested in the local St. Louis issues of bribery and graft. After bribery fell out of fashion, he recognized that it was resurrected, legitimized, and institutionalized and called Political Action Committees or PACs. Aside from the protestations of elected officials, is there any reason to think that contributions do not influence legislation? Until this is addressed, that is until PACs are eliminated, legislative power is going to remain in the interest of large contributors to the detriment of the public at large.

As the bill for the National Biological Survey moved through the House of Representatives in 1993, several real or perceived issues surfaced. The very word Survey in the title conjured up in the minds of some representatives swarms of "Audubon Gestapo" sweeping across the nation to find new dickey birds in order to regulate the use of private property. The main issues were access to private property, written permission to access private property, and the use of volunteers. What I am going to do is briefly outline each problem and relate the Illinois experience.

Access to private property is a complex issue in that it is difficult to keep isolated from the Endangered Species Act (ESA). Under the ESA, there has been a number of highly publicized incidents, often untrue, that purport to have "infringed" on individual freedom. The words used in these cases are "unreasonable restraint." The word of these so-called incidents has spread like ripples on a pond. Mark Twain observed, "A lie is halfway around the world before the truth puts on its shoes." The fact is that the Fish and Wildlife Service obtained injunctive relief under the ESA only four times in six years (Beattie, 1995).

Governmental regulation is butting heads with a new sense of land ownership rights as perceived and defined by the owners. The perception is that access to private property will lead to new and burdensome regulation which, in turn, is seen as a form of uncompensated land-taking. These sentiments are mostly found in rural areas that have not experienced the regulation, that is, zoning, necessary to make urban areas operable and livable.

Since 1917, the Illinois State Geological Survey, Natural History Survey, and State Water Survey have had authority, in statute (1992 Chapter 96 1/2, ¶ 7403(b)(1)), to enter all lands of the state:

> "(1) To investigate and study the natural resources of the State and to prepare printed reports and furnish information fundamental to the conservation and devel-

> opment of natural resources and for that purpose the officers and employees thereof may, pursuant to rule adopted by the Department, enter and cross all lands in this State, doing no damage to private property."

The wording has changed slightly over the years, but the overall authority remains intact. Staff are expected to contact landowners prior to entering because a plastic identification card provides little protection against the rare event of physical or armed intervention. After hearing the reasons for entering property, the landowner often accompanies the scientist and actually assists with the research. Thus, a landowner is converted into a volunteer and one with an enhanced understanding of the importance of our natural resources, particularly on his or her property.

Were there any instances of problems? Of course. I had to deal with one that was precipitated by staffers who failed to clear entry with the landowner. The landowners were senior citizens who were frightened by the presence of unannounced persons. Their concern was exacerbated by recent cattle-rustling activities in the area.

The written permission to access private property issue is, at least in part, a liability question. Written permission is one way of being certain of who is on the land, and liability is considerably less in the case of a trespasser. Obtaining written permission prior to gaining access to private property is possible, but only to a limited extent. Why? More and more rural landowners are proving difficult to identify because of the shift of population toward urban and suburban areas or their relocation to other states or other countries. We live in Piatt County, Illinois, a relatively small county that is largely agricultural in nature. The largest landowner is a foreign corporation with the land in the hands of a local manager. In central Illinois, on a per-acre basis, close to 75% is operated by someone other than the landowner (Gucker, 1995). Alaska has 71% of its farmland under lease. The lowest percentage of leased farmland is in Maine, New Hampshire, and Massachusetts with 17 to 23%. Many biological events are of a short duration and may be long over before it is possible to locate the landowner, much less receive written permission.

The efforts of volunteers are not opposed, per se. The concern is expressed in each of two steps: data gathered by volunteers may be inaccurate because of a lack of expertise; inaccurate data could be used to formulate policy or additional regulation. The argument basically is that volunteers are not as well trained as professional scientists, and even professional scientists have been known to err from time to time. There is also a concern that volunteers may have subtle "white hat" prejudices that would influence the data-gathering process.

Early on, the House of Representatives passed an amendment to the NBS bill that explicitly forbade the use of volunteers. This amendment was not in the tradition or practice of the majority of the adult population of the United States. Although some languages do not even contain a word for volunteer, volunteerism is deeply seated in the American way of life. It is often said that approximately 80% of American adults serve as volunteers. If volunteerism was curbed by legislation, how would our organizations prosper? Consider the impact on churches, scouting, 4-H, hospitals, museums, service organizations, even political campaigns! To deny the NBS access to volunteers via legislation was both discriminatory and distinctly unAmerican.

There are numerous positive examples of data-gathering by volunteers in natural history. NBS examples include the Christmas Bird Count, Breeding Bird Census, Atlas Programs, Project FeederWatch, Hawk Migration Data, Adopt-A-Refuge, Save-Our-Streams, Natural Heritage Data, and the Fourth of July Butterfly Count. It is imperative for us to understand the concerns of some, and special measures must be taken. Data gathered by volunteers must be reviewed by professional scientists, anomalies investigated, and occasionally data sets may have to be discarded. All interpretation of data must be made by professionals.

In November 1994, along came the Contract with America (CONWAM) and, suddenly, we were confronting a horse of another color. Environmental leadership from the White House collapsed, the environmentally sensitive Vice President disappeared in a flash of white light, and new leadership emerged in the Senate and the House. As we look forward to the next presidential election, leading presidential wannabes and a third-party hopeful do not hold promise of anything better. It seems as though a fifth Horseman of the Apocalypse should be added—elected officials.

The NBS problem areas became increasingly difficult and on January 5, 1995, in an attempt to dampen overheated sensibilities, Secretary Babbitt changed the name to the National Biological Service. Subsequently, both houses of the Congress terminated the NBS, but the Senate's version of H.B. 1917 transferred NBS programs to the Natural Resources Science Agency. Unfortunately, the Senate version provides that no funds may be used for surveys, including aerial ones, on private property unless with the explicit written permission of the owner.

What must we do to restore the worth of our sci-

ence in the eyes of the public and legislators? I have a few suggestions to offer for your consideration.

We must capture the data held in our collections in such a way as to make it usable and useful to a broad spectrum of users. The National Biological Information Infrastructure (NBII) was conceived precisely to make this possible through interconnectiveness. For nearly a quarter of a century too many in the profession have been dragging their feet and using an inability to devise a commonly agreed-upon data format to justify inaction. Full computerization of collections data cannot wait until my grandson grows up, even though at ten months he has an early start. There has been a continuing debate about the best hardware and software. As the technology becomes increasingly transparent, this is no longer a matter for valid discussion. Concerns do remain—proper specimen identification, for example. I am torn on this point: one side says make the data available, even if it is not robust, because it will get corrected; the other side says get it right. In 1972, I suggested that data entry could be made at the time of loan return, thus assuring a higher than normal level of reliability. Had that been done consistently by all, the entomologists, who are facing a monstrous task, would be further along.

A second problem area, no pun intended, is that of geographic locality. Older collections, where the locality data is obscure or too broadly drawn, may have to be put aside even though they are of immense historical importance. For current collections I see no reason why global positioning systems should not be employed to provide the level of accuracy necessary for GIS applications.

Some members of the Congress would prefer to eliminate not only aerial surveys but also electronic data-gathering. At first, this seems curious, but even with limited reflection it is clear that what they wish to eliminate is incontrovertible evidence. Just as I once said that GIS would blow your socks off, the same is now true of the blending of satellite imagery and landcover analysis. Before the end of the year we expect to have complete coverage for Illinois. We completed a 10-year change comparison for one county and found that the changes were not what everyone imagined. A loss of farmland was projected, but proved untrue; the actual loss was in forested lands.

Lack of electronic, that is, Internet, accessibility provides an additional and major problem for some organizations. Those not on the Internet with a home page are excluded from a major information interchange. If you do have a home page, keep track of where the queries are originating and the kinds of organizations making the inquiries. For those of us in the governmental realm, it is clear that we must make our data available. Those among you from private institutions may experience a problem at several levels. The curator may wish to make collections data freely available, but the director does not. The director's position is that the institution has an obligation to try to recoup part of its investment in developing the database. This position honors fiduciary responsibility. The reverse situation may occur if the curator refuses to provide collections data. Wayne King refers to this as "curatorial barony." For those among you who believe that your data can be a major source of institutional revenue and that it can support computer operations, you are advised to reconsider for you will experience disappointment. Computer operations are better regarded as part of the infrastructure support necessary to do science rather than as a revenue stream.

The majority of you are systematists and your institution is, I hope, a member of the Association of Systematics Collections. I mentioned the Systematics Resources Working Group (Working Group) previously, and I would like to share some aspects of our first interim report with you. That report will be issued shortly with six recommendations.

The Working Group recognizes the necessity to focus on products rather than process in order to demonstrate the relevance of systematics collections, systematic biology, biodiversity, and biotic inventories. The first recommendation, to establish a home page for ASC, has been accomplished. Two additional recommendations have been implemented by ASC and NBS, the development of a Taxonomic Resource Expertise Directory and a Directory of Research Systematics Collections. Both directories will be available on the Internet through NBII.

The fourth recommendation is to automate essential collections data. The given is that there are insufficient funds to automate all collections data over the short term. The Working Group identified high-priority groups that could serve as demonstration projects for data automation. The high-priority groups are amphibians and reptiles; conifers; freshwater crustaceans; freshwater fishes; mycorrhizal fungi; lepidoptera; lichens; unionid, hydrobiid, and pleurocerid mollusks; nematodes; and orchids. The Working Group fully realizes that this list will not enjoy universal appeal and, therefore, suggests that the list be subject to regular review and revision. It is of interest that the NSF has awarded more than

sixty grants in FY 93 and 94 in these priority groups.

The fifth recommendation is to develop a public document detailing practical applications of systematics as a supplement to Systematics Agenda 2000. Eventually, examples of applications of systematics should be made available on the ASC Home Page. If you would like an outstanding example of efforts along these lines, see *Reinventing Systematics* (Becker, 1995).

The final recommendation is the development of a list of priority needs for training and professional positions. This list will be developed from identified gaps in scientific expertise in critical biological groups with input from the NSF Partnerships for Enhancing Expertise in Taxonomy (PEET).

Look for opportunities to provide baseline information to both the scientific and lay communities. In Illinois we did this through *Our Living Heritage; The Biological Resources of Illinois* (Page & Jeffords, 1991) and *The Changing Illinois Environment: Critical Trends* (Illinois Department of Energy and Natural Resources, 1994). NBS recently did the same in *Our Living Resources* (LaRoe et al., 1995). Once this information is in the public domain it can be used for demonstrating change over time.

The Office of the President appears to have little power beyond that of persuasion and veto. Therefore, it may be foolish to concentrate exclusively on the presidency with regard to elections. It may be far more important to devote energies to congressional elections. Forget party labels and support those that support environmental issues because the current environmental battlefield is the appropriations committees. Be very careful on this point because some may be prohibited from taking advocacy positions, and others may be with institutions that find it unacceptable. Proposed new legislation linking federal grants and advocacy are an added institutional threat (Anonymous, 1995c).

You are required to learn at least the rudiments of politics and the Byzantine pathway that leads to legislation. It is said that lawmaking is similar to sausage making—you should never see it done. It is important to realize that elected officials are interested in science only as a tool to help formulate policy and legislation. You must not ignore the state-level lawmaking because most land-use law is drawn at the state or county level. Lawmaking is complex and politics, or the lack of knowledge, is apparent at virtually every step, and "it isn't over until it's over."

Write, fax, call, or e-mail your elected officials on issues that are important to you. Be persistent. Check to see if your state has a delegation office in Washington. If it does, find out how to make contact and get to know the staffers. They have systems to contact the state delegation in short order. You may be able to convince them to transmit your message to the entire delegation.

I would like to pause to personally thank the Trustees of the Garden for supporting Peter Raven's effective advocacy on behalf of a host of biological matters over the years. Their support did not happen by accident, but through Peter's continuing efforts to educate the Trustees. Peter, for you I offer my first modern-day environmental holy card.

Most of you believe you are educators—educate! If you do not know where to begin, start with 5th and 6th graders. It is imperative to capture their attention before the glands begin to work and they focus on one another. There are a multitude of ways to approach children—exhibits, theater, coloring posters, curriculum development, field trips, and so on. The second priority should be elected officials. Lure them to your institutions and tour the collections—if you cannot attract the legislators, settle for legislative aides. Show them what you have accomplished and share with them what remains to be done. Stress the importance of their ongoing support. Follow up because you need to let them know when something good happens and not just when you desperately need their assistance. Try the same approach on that reluctant dean or vice chancellor for research.

Once in a while you may wish to try an "experimental" field trip. We tried one that examined wetland delineation techniques in a number of different environmental settings. Invitees were a local state legislator, representatives from the Farm Bureau, U.S. Fish and Wildlife Service, the Soil and Water Conservation Districts, U.S. Army Corps of Engineers, and the state Department of Conservation. The learning and understanding process was generated by the field trip participants and not entirely by the trip leaders.

In the end, you must educate everyone. Do not neglect your trustees or board members. Do you need ideas? Walk around this garden because it absolutely abounds in teaching and learning opportunities.

You are familiar with all the reasons for preserving biodiversity, ecosystems, and the environment. They have almost become a mantra and have put some of us in a hypnotic state, even depression, rendering us incapable of action. Our mantra has not worked, not because our reasoning is not logical but precisely because it is. Stephen Meyer (1995) has noted, "The practice of what most academics

consider to be good science is largely antithetical to the practice of politics." It is a lesson that I, and I suspect far too many scientists, forget with astonishing regularity.

We, you and I, are privileged to be participants in the ultimate detective story—understanding the course of evolution of living things. Could there be anything more challenging or more rewarding? I think not. We are also fortunate in that we often have the opportunity to enjoy and appreciate the sheer beauty of the living world. Because we are so privileged and have some higher level of understanding of where the world is headed, we, you and I, have a responsibility level far above that of the average citizen.

Do you want the story to end in desolation, or do you want the next millennium to herald a new sunrise? Tonight, now, I place the responsibility for the shape of the next millennium into your hands.

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ANNALS OF THE MISSOURI BOTANICAL GARDEN: CHECKLIST FOR AUTHORS

1. General Instructions

- ☐ Text is in English or Spanish on numbered pages.
- ☐ Manuscript is typed on one side of nonglossy 8½ × 11 in. paper.
- ☐ At least 1 in. is left as margin all around, except on the first page, which has 3 in. left blank at the top.
- ☐ Three copies of double- or triple-spaced printed manuscript, including abstract, legends, tables, specimen lists, Literature Cited, and footnotes, are enclosed.
- ☐ Manuscript is also submitted on MS-DOS/WINDOWS 3½ in. diskette, as WordPerfect® [preferable] file.
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- ☐ Special typefaces are not used. Common Latin words or phrases are not italicized (e.g., et al., i.e., sensu, etc.).
- ☐ Only names at the rank of genus and below are italicized.
- ☐ Correct accents, umlauts, and other diacritical marks have been included.
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- ☐ A one-paragraph abstract precedes text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
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- ☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.
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- ☐ One paragraph per basionym is used as follows: *Taxon* author, literature citation, type citation, e.g., *Pleurothyrium amplifolium* (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P). Figure 11.
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